PALAEOECOLOGY OF THE LATE TERTIARY FOSSIL OCCURRENCES IN 'E' QUARRY, LANGEBAANWEG, SOUTH AFRICA, AND A REINTERPRETATION OF THEIR GEOLOGICAL CONTEXT

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(With 17 figures and 9 tables)

ABSTRACT

The late Tertiary succession in the vicinity of Langebaanweg, Cape Province, is correlated with the global sea-level changes of that period. The principal fossiliferous elements are the Quartzose Sand Member (QSM) and Pelletal Phosphorite Member (PPM) of the Varswater Formation, which were laid down during the global early Pliocene transgression. The nature of the succession was determined by the physical geography of the region, while the preservation of an unusually large body of early Pliocene sediment in the Langebaanweg area was due to the development at that time of an overlying coastal barrier complex, part of which survived subsequent erosion.

All elements in the succession are fossiliferous in parts. Approximately 230 invertebrate and vertebrate taxa are recorded from the Varswater Formation, in which a variety of marine, freshwater and terrestrial depositional environments are represented. Species assemblages, body part representation and condition of specimens vary according to the facies from which they are derived. The fossils reflect the changing environmental conditions of the late Miocene and early Pliocene, when local temperatures moderated from tropical to temperate, rainfall was changing from a summer to a winter maximum, and woodland vegetation was giving way to more open grasslands and fynbos.

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INTRODUCTION

General

Langebaanweg (18° 9'E, 32° 58'S) is situated in the south-western Cape Province approximately 110 km north-north-west of Cape town, and a little less than 2° north of the most southerly tip of Africa (Cape Agulhas) (Figs 1–2). It is about 13 km inland (north-east) from Saldanha Bay, and 21 km south of the mouth of the (Great) Berg River at St Helena Bay. The settlement originally consisted of little more than a railway siding, but during the Second World War the commencement of phosphate mining operations and the construction of a military airfield enlivened the area.

The phosphate deposits of the area have long been known, and although commercial exploitation commenced in 1943, it was not until 1958 that the occurrence of vertebrate fossils in these deposits was reported (Singer & Hooijer 1958). Since then the area has become one of the most prolific sources of late Tertiary fossils in Africa. Phosphate has been mined in two areas, and both have yielded fossils. Initially mining was confined to an area immediately west of the Langebaanweg railway station. This open-cast mine, known as Baard's Quarry, was relatively small, and although large quantities of fossils were recovered, most are unidentifiable fragments (Hendey 1978a). About 2 km further west is Varswater, a subdivision of the farm Langeberg, where mining also started on a small scale, with few fossils having been recovered. During 1965 a start was made on the New Varswater Mine ('E' Quarry), a comparatively large undertaking which has been the source of the vast majority of fossils from the Langebaanweg area (see Hendey 1970a, 1974a, 1976a, and other publications cited below).

This report deals largely with the fossils and deposits of that part of the 'E' Quarry sequence which comprises the late Miocene/early Pliocene Varswater Formation. In order that this element in the succession be placed in perspective, an account is also given of other late Tertiary deposits in the vicinity. The entire succession is correlated with others on the west coast of southern Africa, and to the record of global sea-level changes.

The emphasis in the palaeontological sections is on the palaeoecology of the Varswater Formation. 'Palaeoecology' was defined by Olson (1962: 134) as referring 'precisely to the ecology at some ancient time or times and thus, strictly, is an interpretation of the once living biological-physical system'. The primary requirement in any such study is the identification of the plants and animals which lived at the time in question. To this must be added a determina-

tion of the prevailing environment, that is, the physical setting and the climate. Only then can the relationships of the plant and animal communities to each other, and to their surroundings, be assessed.

Although comparatively little is known of the vegetation in Varswater Formation times, the geology and fauna of the deposits have already been
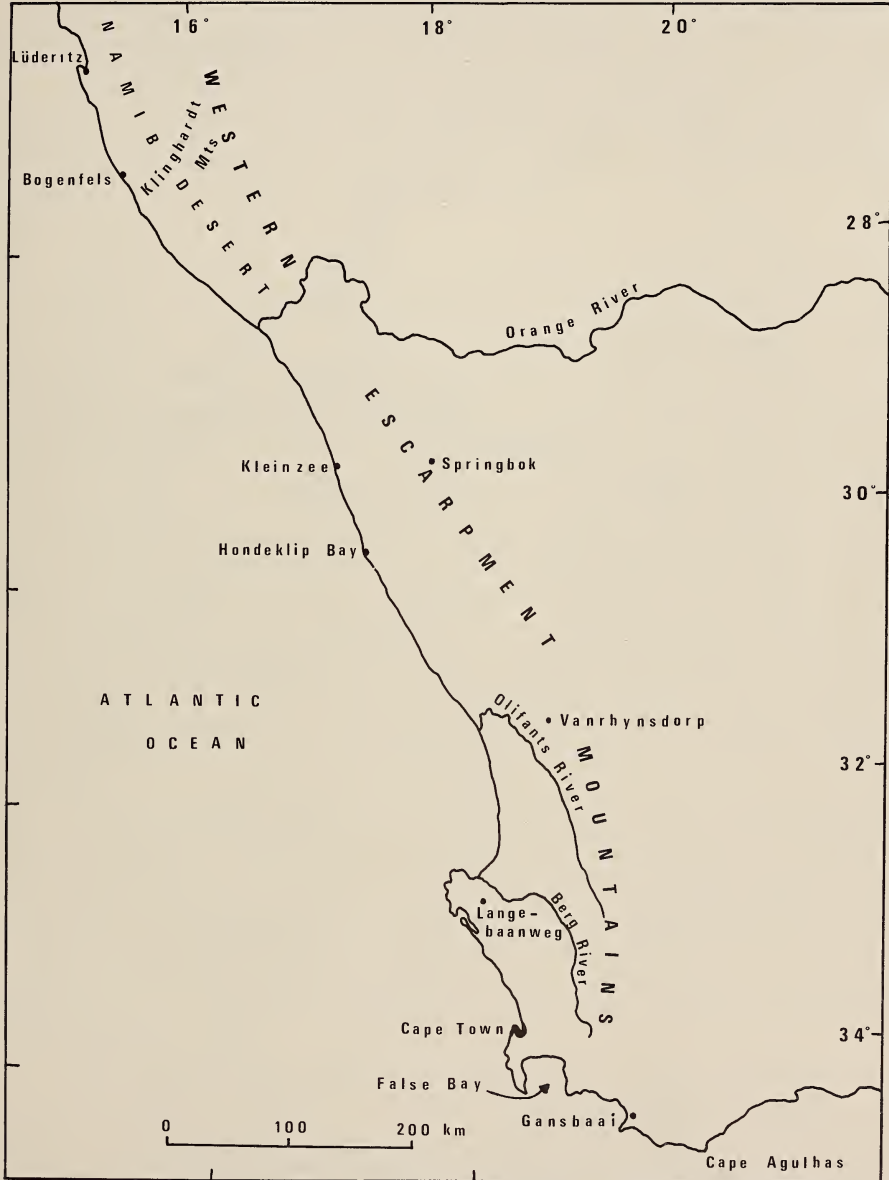
Fig. 1. The west coast of southern Africa.

studied in some detail. Previous publications resulting from these studies have included palaeoecological interpretations, and these are either simply referred to, or the information they contain is repeated here, usually in an abbreviated form. In addition, some previously unpublished observations are included. This synthesis is intended only as an interim report, since relevant research is continuing.

Fig. 2. The Saldanha region of the south-western Cape Province.

While the 'E' Quarry fossils and deposits have already provided a wealth of palaeoecological information, a great deal more is promised by further identification of taxa and detailed analyses of the nature and composition of fossil assemblages from particular horizons or areas. The combination of an unusually rich fauna, some palaeobotanical information, and a complex variety of depositional environments, dating from a period when significant environmental change was taking place, makes 'E' Quarry an excellent subject for palaeoecological studies.

Stemming from the accounts of the geology and biology of the 'E' Quarry deposits is a statement on some evolutionary aspects of the recorded fossil mammals, together with a reassessment of the age of the principal fossil occurrences in the area.

Present environment

The south-western Cape Province has a Mediterranean type of climate (Cs of Köppen), and Langebaanweg is situated in the more arid north-westerly part of this region. Rainfall is brought by the westerly wind system of southern mid-latitudes, which is usually far enough north to affect the area only during winter. Coastal fogs sometimes penetrate to the area during cooler months. The mean annual precipitation is about 250 mm. Winters tend to be cool rather than cold, and very rarely are sub-zero temperatures experienced, and then only at night. The summers are dominated by high-pressure systems in the south Atlantic and are long and dry. Although temperatures may be high (up to 40 °C), they are often moderated by the prevailing south-easterly winds. These winds are frequently moderate to strong, and, being dry, they aggravate the summer aridity by desiccating both the soil and plants. The low temperatures of the adjacent South Atlantic Ocean are caused by an upwelling of Southern Ocean water in the Benguela Current System. This cold water is a major factor contributing to the aridity of the region. A summary account of the climate of the south-western Cape and adjacent regions was given by Fuggle & Ashton (1979).

In the immediate vicinity of Langebaanweg there is no naturally occurring surface fresh water, except for small ephemeral ponds during winter. Otherwise surface fresh water is available locally only at isolated springs, such as that associated with the Quaternary fossil occurrences on the farm Elandsfontein, 20 km to the south-east (Hendey 1974a), or in the Berg River, 15 km to the north-east. The Berg River is perennial and is the largest river in the south-western Cape, draining the major part of this region (Harrison & Elsworth 1958; Harrison 1964).

The sclerophyllous natural vegetation, which has been considerably disturbed by human activity, is classified as 'coastal fynbos', which in this sandy area is 'predominantly ericoid and rather open, the bushes being somewhat rounded and up to 1 m high' (Taylor 1978: 204). Proteoids, restioids, grasses, geophytes, and annuals are present, but there are no indigenous trees. A

detailed account of the vegetation in the near-by area surrounding Langebaan was given by Boucher & Jarman (1977).

The fauna of the area has been depleted during historic times (post-seventeenth century). No larger mammals survive, although smaller ones are not uncommon. They include a variety of insectivores, bats and rodents (including a porcupine), a hare, small carnivores (genets, mongooses, a wildcat, foxes), and small antelope (steenbok, grysbok and probably grey duiker). Birds are both diverse and abundant, nearly 100 species having been recorded in or near 'E' Quarry (G. Benfield, pers. comm.). This is due largely to the artificially well-watered environment created by the open-cast mining, which has extended below the water-table in places. Lower vertebrates include frogs, tortoises, lizards, and snakes. Invertebrates are common and include the land snail, *Trigonephrus*, shells of which are frequently found in local terrestrial deposits of late Cenozoic age.

GEOLOGY

THE LANGEBAANWEG SUCCESSION

The Cenozoic deposits in the vicinity of Langebaanweg have been the subject of many published and unpublished studies, partly because of the economically important phosphate occurrences, and partly because they are in places so richly fossiliferous. At its maximum development the local succession comprises over 100 m of clastic sediments resting on a pre-Mesozoic bedrock. These deposits are largely unconsolidated, and the earliest evidently date back to the early or middle Miocene, followed by a substantial element dating from the Pliocene, while the succession is completed by a nearly ubiquitous covering of Quaternary sands.

The most recent account of this succession, and the only one that deals with it in its entirety, is that of Rogers (1980), whose lithostratigraphy (Table 1) is basically similar to that recognized in earlier studies (e.g. Hendey 1973, 1974a, 1976a, 1980; Tankard 1974a, 1975a, 1975b; Dingle *et al.* 1979). The earlier studies centred largely on the phosphate and fossiliferous deposits of the Varswater Formation (*sensu* Tankard 1974a), which are best known from the exposures in 'E' Quarry.

The 'E' Quarry succession was initially interpreted largely on palaeontological grounds (Hendey 1973, 1974a), and this was followed by detailed studies of the deposits themselves. Tankard's (1974a) definition, description and discussion of the Varswater Formation in 'E' Quarry and adjacent areas is the standard reference on the subject. In a subsequent study, Tankard (1975a) dealt with those deposits underlying the exposures in 'E' Quarry and included them in the 'Saldanha Formation'. He gave a useful review of all the information then available in an unpublished thesis (Tankard 1975b).

The 'E' Quarry succession has since been discussed by Hendey (1976a, 1980), Dingle *et al.* (1979), and Rogers (1980), while the latter two studies also take into account underlying and overlying deposits.

TABLE 1

The lithostratigraphy of Cenozoic deposits in the vicinity of Langebaanweg, Cape Province.

Rogers 1980		This Report	
Formations	Subdivisions	Subdivisions	Age
Bredasdorp	Langebaan Limestone Member (in part)	Surface sands (including duricrusts)	Pleistocene and Holocene
		Baard's Quarry fluviatile deposits	Late Pliocene or early Pleistocene
Bredasdorp .	Langebaan Limestone Member (in part)	Anyskop terrestrial deposits	Late Pliocene
		Anyskop marine deposits	
Varswater .	'phosphorite member' (including beds 3aS and 3aN)	Pelletal Phosphorite Member (PPM) (including beds 3aS and 3aN)	Early Pliocene
	'quartzose sand member' (including 'peat bed' & 'clay bed')	Quartzose Sand Member (QSM) (including floodplain, peat & tidal flat beds)	
	'gravel member'	Gravel Member (GM)	Late Miocene
Saldanha .		Pre-GM deposits	Middle Miocene
Elandsfontyn			

Changes in the nomenclature of the subdivisions of the Varswater Formation have been frequent enough to cause confusion, which is unfortunate since the lithostratigraphy recognized in the various studies has remained virtually unchanged (Rogers 1980, table 3.8). The most distinct of the recent terminologies is that of Dingle *et al.* (1979), and, although it is concise and comprehensive, the largely informal terminology used in all post-1975 palaeontological studies is retained here, with the addition of some completely informal terms which refer to pre- and post-Varswater Formation (*sensu stricto*) deposits.

The latter deposits have hitherto received relatively little attention, and are clearly in need of more detailed study. Only those which have a bearing on the present interpretation of the area's geological history are discussed below.

Since Langebaanweg is located close to the coast, the local succession has been considerably influenced by past changes in sea-level. Although this succession itself provides evidence of the nature and timing of such changes, these can best be interpreted on the basis of regional and global evidence. Consequently, before proceeding to a more detailed account of deposits in the Langebaanweg area, the record of relevant sea-level movements is examined.

TERTIARY SEA-LEVEL MOVEMENTS ON THE WEST COAST OF SOUTH AFRICA

The nature of the Langebaanweg succession is such that it provides some unique data relevant to the interpretation of southern African sea-level movements. However, since the local record is both complemented and supplemented by evidence from further afield, account will be taken here of such evidence from the approximately 600 km west coast of South Africa. This stretch of coast can conveniently be divided into two regions. They are the south-western Cape coast between False Bay and the Olifants River, and the Namaqualand coast between the Olifants and Orange Rivers (Fig. 1). A coastal plain of varying width fronts on a more or less continuous series of mountains, which separates this plain from an inland plateau.

Shorelines of Cenozoic age are preserved along most of this coast, and much attention has been focused on them, mainly because of associated occurrences of phosphate and diamonds. Although particular reference is made to the shoreline successions in the Langebaanweg area of the south-western Cape and the Hondeklip Bay–Kleinzee section of the Namaqualand coast, successions in other areas may be as well known and as relevant.

There are altimetric similarities between the recorded shorelines of the two regions, and correlations between them, and shorelines elsewhere, have been suggested (e.g. Hendey 1969; Carrington & Kensley 1969). The inter-regional correlations have been modified (Tankard 1975b, 1976), while the broader correlations have generally been discounted (e.g. Wolff et al. 1973). While the criticism of the latter correlations was justified, more recent studies have indicated that there is a sound basis for correlating the west coast shoreline succession with global phenomena of the Cenozoic. Consequently, broader correlations are feasible. For example, Tankard (1975b, 1976) has correlated the lower and more recent of the west coast shorelines with high sea-levels of the last interglacial, and it follows that they are the local equivalents of last interglacial shorelines recorded elsewhere in the world.

This aspect of Tankard's studies is irrelevant here, since it is only the older and higher of the late Cenozoic shorelines which are represented in the immediate vicinity of Langebaanweg. According to Tankard (1975b, 1976) the older late Cenozoic shorelines in the south-western Cape are at lower elevations than their counterparts in Namaqualand, this difference being ascribed to differential epeirogenesis along the west coast. However, the difference is here regarded as more apparent than real, and there is, in fact, a remarkable altimetric similarity between all the late Cenozoic shorelines of the two regions.

The Namaqualand succession is both well developed and well documented over a distance of about 400 km, and there has been little disagreement about the elevations of the shorelines constituting this succession. The difference of opinion over the inter-regional correlation centres on the elevation of the higher shorelines in the south-western Cape, and it stems from the nature of the record of these shorelines. The record in the two regions differs simply because of distinctive characteristics in their physical geography.

The Namaqualand coast has a more or less regular north-north-west to south-south-east trend, and, in those areas where ancient shorelines are best developed, it has a bedrock profile which rises at a generally moderate angle from the present shoreline to beyond the limit of the highest late Cenozoic shoreline (*c.* 100 m). The situation is more complex at the mouths of rivers, where marine and river terraces merge, and where fluviatile and estuarine deposits are represented. In general though, the ancient shorelines have a fairly regular development, with associated deposits forming a readily identifiable sequence between 0 and 100 m elevation. The shorelines themselves are generally incised on bedrock. This situation can be largely ascribed to the configuration of the bedrock, and the fact that it is uniformly comprised of 'Namaqualand gneiss' (see Haughton 1968).

By contrast, the coastal area of the south-western Cape is much less regular due to the more complex solid geology (i.e. Basement Complex granites, Malmesbury System metamorphics and intrusives, and Cape Supergroup sedimentary rocks). The more resistant rocks, and those of the relatively young and uplifted Cape Supergroup, form areas of high relief. The bedrock may thus rise steeply from present sea-level to the hills and mountains of the region, although there are also wide areas where bedrock is below present sea-level and where it is overlain by largely unconsolidated late Cenozoic sediments.

The areas of high relief are particularly significant since at times of the higher late Cenozoic sea-levels (*c.* 50 m and above) those in the east would have formed an irregular and often steep-sided coast, whereas those in the west would have formed two island complexes off the southern and central parts of the region. The islands would also have had irregular and steep-sided coasts, and would have provided some shelter to the adjacent mainland coast from the open ocean. Mechanical erosion by wave action on this coast might, therefore, have been reduced.

Shoreline environments in the south-western Cape, both now and at times of past high sea-levels, thus differ appreciably from those of the Namaqualand coast. Consequently, their features and associated deposits are likely to differ in some respects.

In Namaqualand wave-cut platforms on bedrock, on which gravels and other sediments accumulate, often had their onshore limits marked by notches and low cliffs. In other words, they exhibit many of the classic manifestations of 'raised beaches', and are usually easily identified and differentiated.

The situation in the south-western Cape is by no means as simple. In those areas where bedrock is below present sea-level, wave-cut platforms were developed on unconsolidated deposits. They were, therefore, insubstantial and very susceptible to subsequent erosion. In addition, deposits on the platforms were later to intermingle with essentially similar unconsolidated deposits accumulated under very different circumstances (e.g. subaerially, by aeolian action). Furthermore, gravels would not normally have been deposited on these platforms because of the absence of a source-rock, while notches and cliffs

would also have been absent, with impermanent coastal dunes having been present instead. As a result, evidence of past high sea-levels over wide areas in the south-western Cape may be difficult to detect.

In those areas where bedrock rose steeply into hills and mountains, both on the mainland and on the islands, older and higher notches, wave-cut platforms and superimposed deposits would tend to be undercut and eroded away during subsequent periods when sea-level was at lower elevations. In addition, shoreline features developed on the mainland coast in the lee of the two island complexes might have been relatively insubstantial because of lower-energy waves. Consequently, some of the more obvious manifestations of 'raised beaches' may also be obscured in these areas of the south-western Cape.

It is, therefore, not surprising that surveys have found evidence of the older and higher late Cenozoic shorelines in this region either absent or equivocal.

For example, Davies (1973: 722) believed that there was no direct proof of high shorelines in that part of the south-western Cape which includes the Langebaanweg area (Fig. 2), claiming that 'the existence of pleistocene sea-levels at 90 m and 60 m in [this area seems to be] inferred from these levels in Namaqualand'. The existence of a *c*. 90 m marine platform in the vicinity of Elandsfontein south-east of Langebaanweg was suggested by Mabbutt (1956), a view subsequently substantiated by Rogers (1980), although he records marine deposits up to an elevation of only about 80 m. This platform is on unconsolidated sediments and is an example of one which lacks some of the classic features of such platforms. The existence of a 50–55 m high sea-level in the vicinity of Langebaanweg has been demonstrated by Tankard (1974*a*—see p. 40), while Mabbutt (1956: 50) recorded a marine terrace at '45–60 m' 'inland from Saldanha Bay'. This one also lacks the features of the kind that Davies and others have sought.

Davies (1972: 270) also found 'few indications of quaternary shorelines above 30 m' in the southern part of the south-western Cape (i.e. around False Bay and along the southern coast to Gansbaai). However, he does record some evidence of high sea-levels in this area at 45–60 m and 75–94 m. The fact that these records are insubstantial is probably due to the generally precipitous nature of the coast in this area and the destruction of higher shoreline features by subsequent erosion. In addition, the eastern shore of False Bay was sheltered by islands that now constitute the Cape Peninsula.

The fact that there is *some* evidence of these higher shorelines in the south-western Cape is a certain indication that they exist. The evidence for their presence cannot be dismissed because the shorelines are not obvious over wide areas, or because they lack some of the characteristics of shorelines elsewhere. Uncertainty about the actual elevation of the higher shorelines, or discrepancies between recorded elevations in the south-western Cape and Namaqualand do not nullify the correlation between the two regions. They are simply explained by the fact that the south-western Cape record is poorer than that in Namaqualand. In the latter region the stillstands in marine transgres-

sions and regressions are usually determinable, whereas over wide areas of the south-western Cape this is not necessarily the case. In spite of the difference in the nature of the records, elevations for the higher shorelines in the two regions are in remarkably close agreement.

Other Namaqualand shorelines which are supposedly absent or poorly developed in the south-western Cape are those which Carrington & Kensley (1969) recorded at '29–34 m' and '17–21 m'. There is, in fact, unequivocal evidence for a shoreline at c. 30 m in 'E' Quarry at Langebaanweg, while there is an indication of a much later high sea-level at about 20 m in the Langebaan-weg area (see below), which was probably the one responsible for the 15 m marine terrace recorded in the same area by Mabbutt (1956).

It is worth noting in this connection that Tankard (1975b, 1976) has suggested that shorelines recorded at 10 m and 13 m in the south-western Cape may be the equivalent of the 17–21 m shoreline in Namaqualand. He ascribed the lower elevation of the south-western Cape beaches to differential epeiro-genesis on the west coast. Since this factor is dismissed here, the discrepancy must have another explanation. It is possible that the 10 and 13 m records in the south-western Cape represent vestiges of a shoreline at a higher elevation (? c. 20 m), since features associated with shorelines may extend over appreci-able vertical and horizontal distances. Ideally only the maximum elevation of a high sea-level should be recorded (i.e. the shoreline itself), but this is not always possible.

It may be significant that, whereas the 17–21 m shoreline is present and well developed at Hondeklip Bay, it is apparently either not represented at Kleinzee, 80 km further north (Hallam 1964), or its deposits are mixed with, and not distinguishable from, those of the older 30 m shoreline. This may be an indication that the stillstand during which the 17–21 m shoreline was developed was not prolonged, and that, consequently, it was only because of some exceptional circumstance of local geography that sporadic records of it have survived. This would be consistent with the nature of the record of the c. 20 m shoreline in the Langebaanweg area (see below).

The situation on the west coast of South Africa may be summed up by the statement that there is evidence for four relatively high late Cenozoic shore-lines, which are for the sake of convenience referred to by their approximate elevations of 90 m, 50 m, 30 m and 20 m. All represent 'transgressive' or 'regressive complexes' and deposits associated with them may therefore be encountered at elevations above or below those given above.

It has generally been assumed that there is a direct correlation between the age and the elevation of these shorelines, the oldest being the highest, and with elevations decreasing with age. It is evident from the Langebaanweg record that this is not the case. In this area the 30 m shoreline is the oldest, followed in descending order of age by the 90 m, 50 m and 20 m shorelines. The Langebaanweg succession is also important in providing evidence of the actual, or likely, age of these shorelines.

Up until a decade ago it was common practice to suggest correlations between South African shoreline sequences with others elsewhere, notably the classic ones of the Mediterranean Basin, which in turn were correlated with the glacial–interglacial chronology of the Quaternary. Since then the nature and timing of sea-level changes during the late Cenozoic have been much more thoroughly documented, while the complexities imposed by tectonic instability have become more widely appreciated, and the earlier correlations are no longer accepted.

A positive advance in long-range correlation of west coast shorelines came with the studies of Tankard (1975b, 1976), who suggested that most, if not all, of the lower shorelines in the south-western Cape date back to the last interglacial. The validity of this conclusion will not be examined here as none of the shorelines is represented in the immediate vicinity of Langebaanweg. At issue though is the age of the older and higher beaches, which have for the most part continued to be regarded as being of Pleistocene age as well. Vertebrate fossils associated with the higher shorelines in the Langebaanweg area indicate beyond all doubt that this succession is largely, or entirely, late Tertiary in age. In addition, the nature of the Langebaanweg fossil assemblages allows for an interpretation of depositional environments which is in good accord with the late Tertiary sea-level movements around southern Africa recorded by Siesser & Dingle (1981). These are in turn in close agreement with the global sea-level changes which were determined by Vail et al. (1977). Siesser & Dingle (1981: 83) were concerned only with the 'gross movements of the seas around southern Africa during the Tertiary', and details of these movements during the late Tertiary determined on the basis of the Langebaanweg record match those of the global changes (Vail et al. 1977; Vail & Hardenbol 1979) remarkably well (Fig. 3).

Siesser & Dingle (1981: 83) summarized the sea-level movements relevant to the Langebaanweg succession as follows: 'The major Neogene transgression began in the middle Miocene and probably reached its greatest extent in the late Miocene or early Pliocene. The overall middle Miocene to early Pliocene transgression was interrupted by a brief regressive pulse near the Miocene–Pliocene boundary. Seas withdrew again in the late Pliocene.'

The interpretation of global sea-level changes of Vail & Hardenbol (1979) differs slightly in that they have the major Neogene transgression commencing during the early Miocene, reaching a climax early in the middle Miocene, and followed by a middle to late Miocene regression, which took the form of three major drops in sea-level, separated by periods when sea-level was more or less static. The last of these major drops evidently coincides with the 'brief regressive pulse near the Miocene–Pliocene boundary' recorded by Siesser & Dingle (1981: 83).

The sea-level movements which affected the Langebaanweg area are referred to in the discussions which follow as:

1. 'the early to middle Miocene transgression',
2. 'the middle to late Miocene regression', with 'the terminal Miocene regression' climaxing this event,
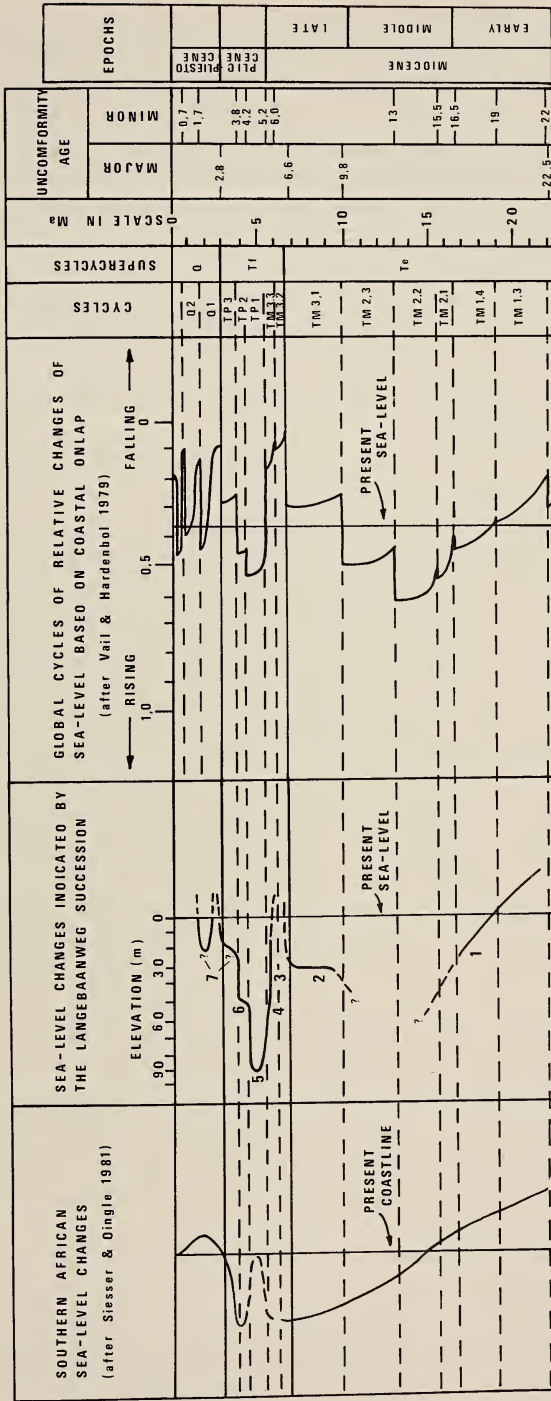
Fig. 3. Records of global and southern African sea-level changes, and those indicated by the Langebaanweg succession. 1. Pre-GM deposits. 2. GM. 3. QSM, PPM. 4. Anyskop marine deposits. 5. Marine platform south-east of Langebaanweg. 6. Anyskop terrestrial deposits. 7. Baard's Quarry fluviatile deposits.

3. 'the early Pliocene transgression',

4. 'the late Pliocene regression' and 'the early Pleistocene transgression'.

According to the present interpretation of the Langebaanweg succession, deposits beneath the floor of 'E' Quarry ('pre-GM') are associated with the early to middle Miocene transgression; the 30 m shoreline (GM) in 'E' Quarry dates from the middle to late Miocene regression; the 90 m shoreline represents the climax of the early Pliocene transgression, with a large proportion of the deposits in the immediate vicinity of 'E' Quarry having been laid down during this transgression; while the 50 m shoreline represents a stillstand in the late Pliocene regression. The 20 m shoreline is problematical, having been developed either during a second stillstand in the late Pliocene regression, or at the climax of the subsequent early Pleistocene transgression. The reasons for this interpretation will become evident from the discussions which follow in this, and later, sections of this report.

On the basis of the altimetric correlation of south-western Cape and Namaqualand shorelines, it follows that the 29–34 m shoreline in Namaqualand must be of late Miocene age. Carrington & Kensley (1969) believed this shoreline dated from the middle Pleistocene, but there is no firm foundation for this suggestion. The 29–34 m shoreline is represented at Hondeklip Bay, where it is 'thin' and 'discontinuous' (Carrington & Kensley 1969: 190), and at Kleinzee (Hallam 1964), where it is also poorly developed (personal observation). This poor development sets it apart from other elements in the Namaqualand, succession, which suggests that it might have been subjected to erosion during a *subsequent* period when sea-level was at a higher elevation. In other words, it is likely to pre-date the 90 m and 50 m high sea-levels, rather than post-date them as suggested by Carrington & Kensley (1969).

Again on altimetric evidence, the early Pliocene 90 m, late Pliocene 50 m, and the late Pliocene/early Pleistocene 20 m shorelines in the south-western Cape are correlated with the '75–90 m', '45–50 m' and '17–21 m' 'transgressive complexes' in Namaqualand, which Carrington & Kensley (1969: 190–191) dated as 'Basal', 'Lower' and 'Middle Pleistocene' respectively.

According to the above interpretation of west coast shorelines, there are none of middle Pleistocene age. There undoubtedly were glacio-eustatic sea-level fluctuations during this period, and it is likely that during the interglacial phases sea-level was higher than at present, just as it was during the last interglacial, and apparently also during the mid-Holocene. However, Shackleton & Opdyke (1973) have suggested that middle Pleistocene interglacial sea-levels would have been no higher than the highest of the last interglacial levels. Consequently, in tectonically stable area all traces of their presence might have been obscured or destroyed during the last interglacial.

Coastal deposits about which there is some uncertainty are those in the Hondeklip Bay area which in mining terminology are referred to as 'E stage' (Tankard 1975b). Although they, too, relate to periods of higher sea-level, they have been regarded as distinct from the deposits of the 'transgressive com-

plexes', and both Carrington & Kensley (1969) and Tankard (1975b) dated them as late Tertiary. Since the higher of the 'transgressive complexes' are here also regarded as late Tertiary, it is necessary to reconsider the age and relationships of the 'E stage' deposits.

The 'lower E stage' deposits were correlated by Tankard (1975b) with the middle Miocene phosphatic rock horizon in 'E' Quarry at Langebaanweg. This correlation is accepted here and the 'lower E stage' is regarded as remnant evidence for the early to middle Miocene transgression on the Namaqualand coast.

The 'middle E stage' deposits were correlated by Tankard (1975b) with the QSM of the Varswater Formation, and this is also accepted here, although the correlation is extended to include the PPM of the Varswater Formation. The QSM and PPM date from the same episode (i.e. the early Pliocene transgression), and there are no grounds for believing that the 'middle E stage' is contemporary with the QSM rather than the PPM.

The age of the 'middle E stage' was partly inferred from remains of two vertebrate taxa which were believed to be derived from this 'stage' and redeposited in younger sediments. One of these taxa, *Ceratotherium praecox*, is represented by a single rolled tooth (Hooijer 1972), which almost certainly is a derived specimen (A. J. Carrington, pers. comm.). The second, '*Prionodelphis*' (= *Homiphoca*) *capensis*, is represented by an isolated canine and a metatarsal. They are unrolled, but Carrington believed them to be derived since they are phosphatized specimens from non-phosphatic deposits. This is not a convincing point of view since phosphatized fossils *in situ* in non-phosphatic deposits have been recorded from 'E' Quarry. A new development concerning the Namaqualand '*Homiphoca capensis*' is that the metatarsal has been found to be appreciably longer than any of the now numerous specimens known from 'E' Quarry. This suggests that the Namaqualand specimen represents a species which was more advanced than the 'E' Quarry *H. capensis*. Consequently, it may well be contemporaneous with the post-'middle E stage' deposits from which it and the isolated canine were recovered.

Other deposits on the Namaqualand coast which were a likely equivalent of the 'middle E stage' were those at Kleinzee from which was recovered the small vertebrate fauna described by Stromer (1931a, 1931b). This fauna is evidently broadly contemporaneous with those from the QSM and PPM at Langebaanweg (Hendey 1974a, 1978c, 1978d).

The 'upper E stage' deposits in the Hondeklip Bay area contain pelletal phosphorite, which led Tankard (1975b) to correlate it with the PPM of the Varswater Formation. While this interpretation cannot be discounted, it is not favoured here. According to one interpretation, the 'E' Quarry pelletal phosphorite is largely derived from a 'mechanical erosion' of the 'Miocene bedded authigenic phosphorite' (Tankard 1975c: 375), and there is no reason to believe that a similar deposit on the Namaqualand coast is necessarily contemporaneous. While it, too, might have been derived from a Miocene phosphorite, the

erosion process in Namaqualand could well have pre- or post-dated deposition of the Varswater Formation PPM. The same applies if the 'upper E stage' and 'E' Quarry pelletal phosphorites are authigenic.

Tankard (1975*b*) records that the 'upper E stage' sediments contain a rich fossil fauna, the molluscs of which indicate warm-water conditions, and that the sediments are recorded only up to an elevation of 30 m. Perhaps significantly, the GM of the Varswater Formation is also comprised of a mechanically eroded Miocene phosphorite, although in the form of a gravel rather than pellet-sized particles, it is also associated with a warm-water mollusc fauna (see p. 68), and it also occurs up to an elevation of 30 m. By contrast, the PPM contains an element which suggests cold-water conditions, and is recorded at elevations well above 30 m.

The 'essentially bedrock-depression infilling' 'upper E stage' (Tankard 1975*b*: 277) may, in fact, represent a part of the 'thin, discontinuous' '29–34 m beach' of Carrington & Kensley (1960: 190), and is recorded as such in Table 2.

The temperature of the adjacent ocean at the time that the various elements in the west coast succession were laid down is of interest. The revised interpretation of the Namaqualand succession means that all those deposits from which warm-water mollusc faunas are recorded date back to the late Tertiary, while those with cold-water faunas are Quaternary.

There are, however, apparent exceptions to this general rule. The 75–90 m shoreline deposits in Namaqualand are unfossiliferous (Tankard 1975*b*), and consequently provide no direct evidence of water temperatures prevailing at that time. However, deposits laid down in 'E' Quarry during an early stage in the 90 m transgression (i.e. the QSM and PPM) contain fossils that indicate cold-water conditions (see p. 68). There is thus likely to have been a similar cold-water fauna on the Namaqualand coast at that time. This period of cold is correlated with the aftermath of the Antarctic glacial maximum during the terminal Miocene (see p. 70). Since the 90 m early Pliocene transgression post-dates this glacial maximum, it is possible that cold conditions prevailed only during the early stages of the transgression, and that by the time it reached its peak sea temperatures were higher.

Tankard (1975*b*) recorded that the 17–21 m shoreline in Namaqualand is associated with a cold-water fauna. If this shoreline is late Pliocene in age, then it would be an exception to the 'late Tertiary/warm water' rule. On the other hand, this may be interpreted as evidence that the 17–21 m shoreline dates from the early Pleistocene, which would be in keeping with evidence from the Langebaanweg area (see p. 41).

Although the present study was confined to the shorelines on the west coast of South Africa, it is obvious that a similar reinterpretation of coastal sucessions elsewhere in southern Africa is possible. For example, according to the present interpretation and contrary to earlier opinion, the 'Upper Terraces Group' on the southern coast of the Namib Desert, with their warm-water faunas (Hallam 1964), are likely to be late Tertiary in age.

TABLE 2

Records of late Tertiary and early Pleistocene sea-level changes on the west coast of southern Africa.

AGE	TRANSGRESSION OT REGRESSION	SEA-LEVEL CYCLES (1)	SOUTH-WESTERN CAPE (2)	HONDEKLIP BAY (3)	KLEINZEE (4)	SOUTHERN NAMIB DESERT (4), (5)
Early Pleistocene	T	QI	20 m (Baard's Quarry fluviatile)	17–21 m	? in part←	?←
Late Pliocene	R	TP3	?	?	?	?
		TP2	50 m (Anyskop terrestrial)	45–50 m	40–64 m	15 m (E Beach)
Early Pliocene	T	TP1	90 m ('E' QSM, PPM; Anyskop marine)	75–90 m (? including 'middle E stage)	82–88 m	20–25 m (F Beach)
Terminal Miocene	R	TM3.2, TM3.3	No deposits	No deposits	No deposits	No deposits
Late Miocene	R	TM3.1	30 m ('E' GM)	29–34 m (? including 'upper E stage')	21–40 m	12 m (D Beach)
Middle Miocene	T	TM1.3–TM2.2	Pre-GM	'lower E stage'		33 m ('false bed-rock gravels' and Arrisdrift fossil site)

(1) Vail & Hardenbol (1979). (2) Langebaanweg area (this report); complementary data from Davies (1972, 1973), Tankard (1974a) and Rogers (1980). (3) Carrington & Kensley (1969) and Tankard (1975b). (4) Hallam (1964) and Corvinus & Hendey (1978). (5) Downwarped coast — terraces at lower elevations than those on South African coast.

The poorly developed 'D Beach' (12 m) of the 'Upper Terraces Group' is here tentatively correlated with the late Miocene 30 m shoreline on the South African west coast, although it could instead be the equivalent of the late Pliocene 20 m shoreline. The latter alternative is less likely because the 20 m shoreline is apparently associated with a cold-water fauna (see above). In addition, the poor development of the 'D Beach' may be an indication of erosion during a subsequent high sea-level, which was suggested in the case of the 30 m shoreline on the South African west coast.

The 'F Beach' (25 m) and 'E Beach' (15 m) are here correlated with the South African west coast 90 m and 50 m shorelines.

The 'false bedrock gravels', which extend northwards from the mouth of the Orange River, evidently pre-date the 'Upper Terraces' (Hallam 1964), and could therefore date back to the middle Miocene. They are the likely equivalent of the pre-GM deposits at Langebaanweg and the 'lower E stage' of the Namaqualand coast. In addition, they are probably the coastal equivalent of the middle Miocene river terrace(s) at Arrisdrift, 30 km inland from the mouth of the Orange River (Corvinus & Hendey 1978; Hendey 1978b). It is worth noting in this connection that the bedrock elevation of the channel which contains the middle Miocene fossils at Arrisdrift is 40 m, while the river level is 7 m above sea-level. It follows that their coastal equivalent should be at 33 m, which is, in fact, the elevation of the base of the cliff against which the 'false bedrock gravels' are banked (Hallam 1964). It may also be significant that while there are four river terraces recognized at Arrisdrift (Corvinus & Hendey 1978), there are also four marine terraces of late Tertiary age on the coast (i.e. the 'D', 'E' and 'F' Beaches and the 'false bedrock gravels').

The Arrisdrift fossil occurrence is of particular significance in the interpretation of the southern African west coast succession, since it provides the most reliable evidence of the time at which the early to middle Miocene transgression began to result in deposition on the present coast. The Arrisdrift fossils date back about 16 Ma (Hendey 1978b), that is, to the early part of the middle Miocene.

The correlation of the west coast shorelines suggested here is summarized in Table 2.

GEOLOGICAL HISTORY AND DEPOSITIONAL ENVIRONMENTS OF THE LANGEBAANWEG SUCCESSION.

As indicated earlier, the Langebaanweg succession is most conveniently interpreted in relation to the southern African sea-level changes recorded by Siesser & Dingle (1981).

The pre-Miocene sea-level changes

There is no evidence in the Langebaanweg area (Figs 2,4) for any deposits dating back to the early Tertiary. Two marine transgressions are recorded
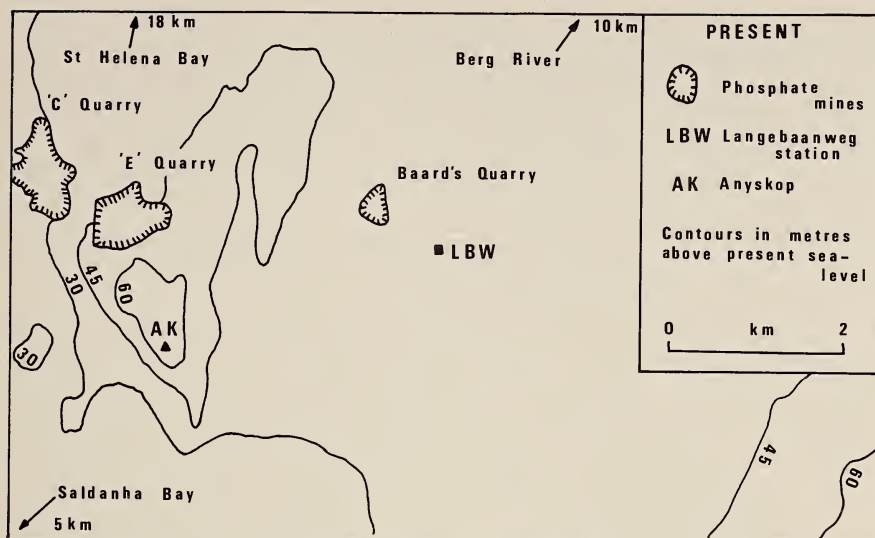
Fig. 4. The Langebaanweg area today.

during this period, one in the late Paleocene/early Eocene and the other in the late Eocene (Siesser & Dingle 1981).

There are records of Eocene marine deposits at 70 and 163 m on the west coast in the southern Namib Desert (Bogenfels and Buntfeldschuh—Siesser & Dingle 1981), as well as possible Eocene deposits at about 140 m at Buffels Bank (Kamaggas) west of Springbok (South African Museum records), and of uncertain elevation at Quaggaskop near Vanrhynsdorp (Lamont 1947). If the latter records are indeed Eocene, then the shorelines of this period must have abutted the western escarpment in Namaqualand, whereas in the downwarped southern Namib they approached the present coast near Bogenfels following the east–west trend of the Klinghardt Mountains in this area (Fig. 1). The implication is that during the Eocene transgressions much of the south-western Cape, including the Langebaanweg area, was below sea-level, the coastline being along higher ground many kilometres east of Langebaanweg.

There was then a major regression spanning the entire Oligocene, and much or all of the early Miocene, when sea-level reached several hundred metres below that of the present (Siesser & Dingle 1981). This is likely to have been the period of major continental erosion during which all traces of early Tertiary sediments in the Langebaanweg area, and elsewhere along the west coast, were removed. It might have been during this period that the bedrock in the Langebaanweg area was eroded down to its present elevation of about −40 m.

The early to middle Miocene transgression

The presence of early Miocene vertebrates in fluviatile and lacustrine deposits near the coast of South West Africa between Bogenfels and Lüderitz

(Stromer 1926; Hopwood 1928; Hamilton & Van Couvering 1977; Hendey 1978b) is a possible indication that at least this section of the west coast was then being influenced by the early to middle Miocene transgression. The southern Namib region was certainly being influenced by this transgression early in the middle Miocene, when the fossil assemblage at Arrisdrift was deposited on a river terrace (Corvinus & Hendey 1978; Hendey 1978b). Apparently contemporaneously the 'false bedrock gravels' of the southern Namib coast were being laid down, and these are in turn correlated with the 'lower E stage' and related deposits on the Namaqualand coast, and the pre-GM deposits in the Langebaanweg area.

The pre-GM deposits are known only from boreholes, although small exposures of their uppermost levels formerly exised in 'C' and 'E' Quarries. About 70 m of these deposits are now known, ranging in elevation from about −40 m to +30 m (Rogers 1980), although until recently only the upper 15–20 m had been placed on record (Tankard 1975b). The sequence is apparently comprised largely of deposits laid down under terrestrial environments, but at least in the case of the upper levels studied by Tankard (1975b: 34), 'it is likely that these deposits formed close to sea level' during 'a slow transgression'. Tankard found evidence in the sequence of a 'marine incursion', which was 'a minor event of very short duration . . . readily explained by breaching of a barrier'. A second marine incursion 'was accompanied by phosphate minerali-zation to form a phosphatic sandstone' (Tankard 1975b: 34).

Peats in the succession have yielded abundant pollens which indicate a forested environment, including subtropical elements such as palms (J. A. Coetzee, pers. comm.), which was very different from the treeless sclerophyll (fynbos) vegetation of the area today. Macroplant remains also include rem-nants of trees. The plant fossils provide no direct evidence of age, but the vegetation is consistent with a local one of Miocene age (Coetzee 1978).

The phosphatic sandstone mentioned above is recorded up to an elevation of 30 m, and is a significant element in the succession. It contributed to Tankard's (1975a: 262) dating of at least this element as 'middle Miocene (Langhian)', and provided some indication of the likely marine environment at the time that it was developed (Tankard 1974a; Birch 1977). In addition, its resistant nature served to protect the underlying deposits from erosion during the marine regression that followed during the late Miocene.

The 30 m elevation of the phosphatic sandstone recorded in 'E' Quarry does not necessaily reflect the maximum elevation reached by the early to middle Miocene transgression. If this phosphatic rock formed in an open shelf environment as suggested by Birch (1977, fig. 4), then the 'E' Quarry area might have been as much as 200 m below the sea-level of that time.

Another indication that this transgression reached an elevation substan-tially higher than 30 m is the presence on the southern Namib Desert coast of apparently contemporaneous deposits at 33 m (Table 2). It is evident from the elevations of the late Tertiary shorelines post-dating the 33 m terrace that there

has been appreciable downwarping of this coast. For example, the suggested equivalent of the 90 m early Pliocene shoreline on the South African west coast is at an elevation of only 20–25 m in the southern Namib Desert, and drops to even lower elevations northwards from the Orange River (Table 2; Hallam 1964). The implication is that the 33 m terrace is now also much lower than its as yet unrecorded counterpart on the South African west coast.

It is, therefore, unlikely that the 30 m record at Langebaanweg and the 33 m record in the southern Namib represent the maximum elevation of the early to middle Miocene transgression. There is apparently no way of determining this elevation on the basis of available evidence, and this is reflected in the Langebaanweg record represented in Figure 3. However, it is possible that the ?Eocene marine deposits at Buffels Bank and Quaggaskop in Namaqualand (see p. 19) are, in fact, of middle Miocene age. The former are at an elevation of about 140 m, and although the elevation of the Quaggaskop deposits is uncertain, it is apparently about 120 m. The middle Miocene transgression might therefore have reached an elevation in the order of 120–140 m.

The middle to late Miocene regression

The middle to late Miocene regression affected the Langebaanweg area by causing erosion of deposits laid down during the preceding transgression. The middle Miocene phosphatic sandstone exposed in 'C' and 'E' Quarries, and encountered in boreholes to the south and south-west of these quarries, was reduced by wave action to a gravel comprising pebble-, cobble- and boulder-sized elements. The north-easterly limit of this gravel, which was briefly exposed in trenches on the floor of 'E' Quarry during 1972, occurs at an elevation of about 30 m. The gravel itself forms the basal unit of the Varswater Formation (i.e. the Gravel Member—GM).

The GM evidently had a complex history. For example, Butzer (1973: 238) recognized five stages in its development, excluding the formation of the original phosphatic sandstone. They are:

1. 'Reworking of [the primary middle Miocene] phosphatic rock.'
2. 'Induration of the previous agglomeration with phosphate' to form what is here termed the secondary phosphatic rock of the GM (Fig. 5).
3. 'Reworking of this new generation of [phosphatic rock] into cobbles and blocks.'
4. 'Partial carbonate cementation and iron-enrichment of the previous agglomerate'.
5. 'Reworking of all the previous products of induration into a matrix of unconsolidated, white (10YR) medium-to-coarse-grade sands.'

Assemblages of marine fossils indicative of sandy and rocky beach environments occur in the secondary phosphatic rock (stage 2), and in the unconsolidated sands (stage 5). These were termed 'Marine Faunal Units 1 and 2' respectively by Hendey (1974a), and their invertebrate components were
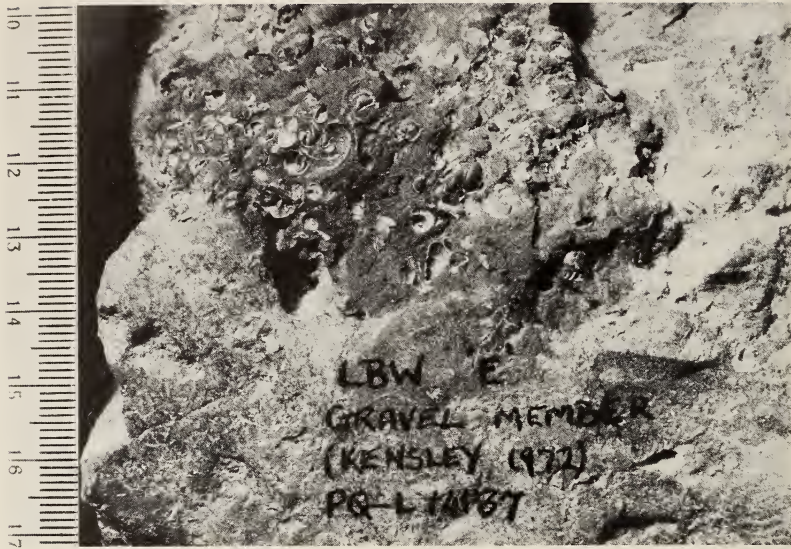
Fig. 5. A Gravel Member (GM) boulder of primary phosphatic rock (labelled section), encrusted with fossiliferous secondary phosphatic rock.

described by Kensley (1972), with some additional taxa having been recorded by Tankard (1974*a*, 1975*b*).

Evidently an appreciable period of time elapsed between stages 1 and 5 in the development of the GM, and throughout this period the deposits must have been at, or near, sea-level. Since the primary phosphatic rock might also have been formed in a similar environment, it is possible that sea-level was at an elevation of about 30 m for much of the middle to late Miocene.

However, this interpretation is not favoured and it seems much more likely that the early to middle Miocene transgression, during which the primary phosphatic rock was formed, reached a much higher elevation, as indicated above.

Another possible interpretation of the history of the GM is that it developed during a temporary stillstand in the middle to late Miocene regression. According to Vail & Hardenbol (1979) this regression was interrupted by two periods when sea-level was nearly static, one between 13 and 10 Ma (cycle TM2.3 of supercycle Te), and the other between 10 and 6,6 Ma (cycle TM3.1 of supercycle Te). Sea-level during the former period was comparable to that during the Langhian (Vail & Hardenbol 1979: fig. 8), the age when the primary phosphatic rock was formed (Tankard 1975*a*), and this coincidence, coupled with the coincident occurrence of the primary and secondary phosphatic rocks in 'E' Quarry, may indicate that the GM dates from cycle TM2.3. On the other hand, the elevation of the GM relative to that of subsequent high sea-levels recorded in the Langebaanweg area suggests that the GM was developed during the cycle TM3.1, that is, immediately prior to the terminal Miocene regression.

It is also possible that one or more of the later stages in the development of the GM took place during the subsequent early Pliocene transgression. While this possibility cannot be dismissed, it is not favoured here, because both invertebrate assemblages of the GM include warm-water taxa, suggesting sea temperatures consistent with the late Miocene, whereas at least during the early stages of the early Pliocene transgression sea temperatures were lower (see p. 16). In addition, the repeated reworking of previous products of deposition observed by Butzer (1973) is more consistent with a regression than a transgression.

A considerable amount of attention has been focused on the origin and age of phosphatic deposits, including those in South Africa (e.g. Tankard 1974b; Birch 1977; Siesser 1978) and further investigation of the primary and secondary phosphatic rocks of the GM may provide additional evidence relevant to the history of this horizon. Tankard's (1975a) belief that the phosphatic rock horizons on the west coast are all of middle Miocene age is now discounted (Siesser 1978; Dingle et al. 1979). This probably is indeed the age of the primary phosphatic rock represented in the GM, but the secondary phosphatic rock may be appreciably younger. Siesser (1978) has concluded from evidence on the South African continental shelf that phosphate deposition also occurred during the late Miocene and into the Pliocene. Although there is at present no direct evidence linking this period of phosphate deposition with the secondary phosphatic rock, such a link would be consistent with the inferred late Miocene age of the GM.

It was suggested elsewhere (Hendey 1976a) that the GM includes some fossils derived from pre-existing deposits. This suggestion was based on the belief that the GM was broadly contemporaneous with the overlying QSM and PPM, and the presence in the GM of some teeth tentatively identified as belonging to the late Miocene horse, *Hipparion primigenium* (Hendey 1976a), which is distinct from the *H*. cf. *baardi* and *H*. cf. *namaquense* found in overlying deposits (Hooijer 1976). However, now that the GM is interpreted as a late Miocene deposit, the *H*. cf. *primigenium* teeth may well be contemporaneous with its deposition. If so, then the GM can be no older than 12,5 Ma, the earliest date at which *Hipparion* could have entered Africa (Churcher & Richardson 1978).

The reworking and accumulation of deposits constituting the GM ceased with the retreat of the sea from the Langebaanweg area, probably at the time of the terminal Miocene regression. Tankard (1974a) suggested that this retreat was caused by the development of a sandbar to the south of 'E' Quarry during a temporary stillstand in the transgression which led to the deposition of the Varswater Formation. Tankard has demonstrated that such a bar did, indeed, exist during the period of deposition of the QSM and PPM, while it is certain that these elements in the succession were deposited during a transgression. However, the stillstand postulated by Tankard is here interpreted as a regression (i.e. the terminal Miocene one), and it is believed that the bar was built up

only during the subsequent transgression (i.e. the early Pliocene one), when a river began feeding sediment into the area.

The interpretation of the sea-level history at that time as 'transgression–regression–transgression' over a prolonged period, rather than a shorter period of 'transgression–stillstand–renewed transgression', was the key to the correlation of the 'E' Quarry succession with certain global events of the late Miocene and early Pliocene (see p. 70). This, in turn, suggested a correlation with the record of sea-level movements around southern Africa as interpreted by Siesser & Dingle (1981), and to the global sea-level changes recorded by Vail *et al.* (1977) and Vail & Hardenbol (1979).

Hitherto the deposits of 'E' Quarry have been interpreted as having been laid down during a single transgression, probably that which resulted in deposition of Dingle's (1971, 1973) unit T_4 (e.g. Bishop 1980). The revised interpretation of events indicates that while the QSM and PPM are referable to T_4, the underlying deposits correlate with unit T_3. These units are respectively correlated with sea-level supercycles Tf and Te of Vail & Hardenbol (1979).

The early Pliocene transgression

Introduction

Whatever the history of the GM and the period immediately following its deposition, it is clear that thereafter there was a major change in the local environment. This was brought about by another marine transgression, during the early stages of which a river met the sea in the immediate vicinity of 'E' Quarry and was responsible for discharging most of the sediment making up the QSM and PPM of the Varswater Formation. The nature of these sediments was dependent on the position of the river channel, which moved northwards as the transgression progressed.

The QSM and PPM are by far the best documented deposits in the Langebaanweg area (Table 3). The largest assemblages of fossils from this area are from these deposits and they provide the evidence of age (*c.* 5,0 Ma) which indicates their association with the early Pliocene transgression (see p. 94). Judging from fossil evidence and the likely relationship of these deposits to others in the vicinity, the QSM and PPM date from the earlier part of this transgression. The earliest phase in this transgression is not represented by deposits in the area, while towards its climax the area was largely, or entirely, inundated by the sea. The only surviving record of local deposition during the latter period are some of the deposits making up Anyskop, which overly the PPM south of 'E' Quarry.

Three distinct positions have been recognized for the lower course of the river during the period of deposition of the QSM and PPM. There were intervals of undetermined duration between the successive positions of the river channel. These intervals are reflected by evolutionary changes in taxa common to more than one set of deposits associated with the channel positions (Hendey 1978*d*, 1980; Gentry 1980; De Muizon & Hendey 1980).

When the QSM was laid down, the river channel was to the south-east and south of 'E' Quarry, its estuary being immediately north of the sand-bar recorded by Tankard (1974a) (Figs 6–7). The configuration of the estuary and the bar separating it from the sea was then probably similar to the analogous area of the Berg River today, the principal difference being in the position of the sea relative to the estuary. The sea is to the north of the present estuary, which has a north-east to south-west trend, but in QSM times the bar had a more or less east to west trend, with the sea to the south.

The second position of the channel was about 500 m further north, and it cut diagonally across 'E' Quarry from north-east to south-west. The northward movement of the channel was probably caused by the transgressing sea breaching the sand-bar. The fossiliferous deposits of the second channel constitute bed 3aS of the PPM, while other largely unfossiliferous deposits make up part of the undifferentiated element of the PPM. These deposits were laid down over the QSM, filling the area north of the original bar. The extent of the bar was thus considerably increased, both vertically and horizontally (Fig. 7). The sea-floor beyond the river mouth was marked by a submarine channel (Fig. 6).

Later still the channel shifted northwards again, but this time the change was slight. It might have affected only a relatively short section of the river, perhaps as little as the last kilometre from its mouth, with the mouth itself probably remaining in essentially the same position as in bed 3aS times. The new channel still had a north-east to south-west trend, although once beyond the northern perimeter of the quarry it swung southwards and truncated the south-westerly parts of bed 3aS (Fig. 6). The deposits of the third channel, and associated fossiliferous ones, constitute bed 3aN of the PPM, and once again contemporary unfossiliferous deposits are included in the undifferentiated element of the PPM.

Thereafter, the river must have continued to discharge sediment (PPM undifferentiated) into the area for a while, but as the transgression progressed, the river mouth must have moved further north or east from the 'E' Quarry area, with a consequent diminution in the influence of the river on local sedimentation. At the time of the climax of the transgression (90 m), the river mouth must have been many kilometres away. The final extent of local deposition at this time cannot be determined since the PPM in 'E' Quarry, and to the north and east, was truncated to a maximum of 50–55 m by erosion during the subsequent late Pliocene regression. The only other recorded local deposits dating from the early Pliocene transgression were some of those comprising Anyskop (see below).

It has previously been assumed that the progressive northward shift in the river channel during QSM and PPM times was caused by the rise in sea-level during the transgression. A second factor involved may have been the build-up in a northerly direction of the sand-bar separating the estuary from the sea. Substantial sedimentation was then taking place, and this, together with the rising sea, might have affected the lower course of the river, especially in the case of the slight change from bed 3aS to bed 3aN.

TABLE 3

Depositional environments, characteristic sediments and fossil occurrences in the QSM and PPM of the Varswater Formation, 'E' Quarry, Langebaanweg.

Dingle et al. 1979	Hendey 1980 and this report			Depositional Environments	Characteristic Sediments	Fossil Occurrences
A–C D1	PPM, undifferentiated			marine littoral	phosphatic sand	some marine microfossils, vertebrates very rare
D3	PELLETAL PHOSPHORITE MEMBER	PPM bed 3aN	I	river bank	clayey sand on phosphate rock	fossils abundant; seals and terrestrial vertebrates predominant
D3			II	river channel	quartz sand and fossil lag on, and in lee of phosphate rock	fossils abundant; seals and terrestrial vertebrates predominant
D2			III	intermediate between II and IV	quartz sand and fossil lag grading into carbonaceous sand and clay	fossils common; seals and terrestrial vertebrates predominant
D2			IV	marsh and pond	carbonaceous sand and clay, sometimes under quartz sand and clay horizons	fossils progressively less common south of III; only vertebrates recorded, but pollens probably present
D4		PPM, bed 3aS	not sub-divided	river channel and river bank	quartz sand and fossil lag grading upwards into phosphatic sand	fossils abundant, but becoming less common in phosphatic sand; terrestrial vertebrates predominant

		QSM			
QUARTZOSE SAND MEMBER	E1	I	floodplain, with associated microenvironments (e.g. pond, minor drainage channel)	quartz sand	fossils sometimes abundant; terrestrial vertebrates predominant
		I(A)	possible variation of I, ? floodplain closer to river channel	quartz sand	fossils sometimes common; terrestrial vertebrates predominant
	E2	II	marsh	carbonaceous sand and clay	fossils abundant; pollens predominant, terrestrial vertebrates common
	E3	III	tidal flats	muddy silt	fossils abundant; marine, estuarine and freshwater invertebrates predominant
	E4	(IV)	? river channel (not exposed but probably exists south-east and south of quarry)	not known	not known

Note. The subdivisions D2 and D3 and E1 to E4 (and their equivalents, PPM 3aN I to IV and QSM I to IV) are facies of sedimentary units (see Dingle *et al.* 1979, fig. 5).
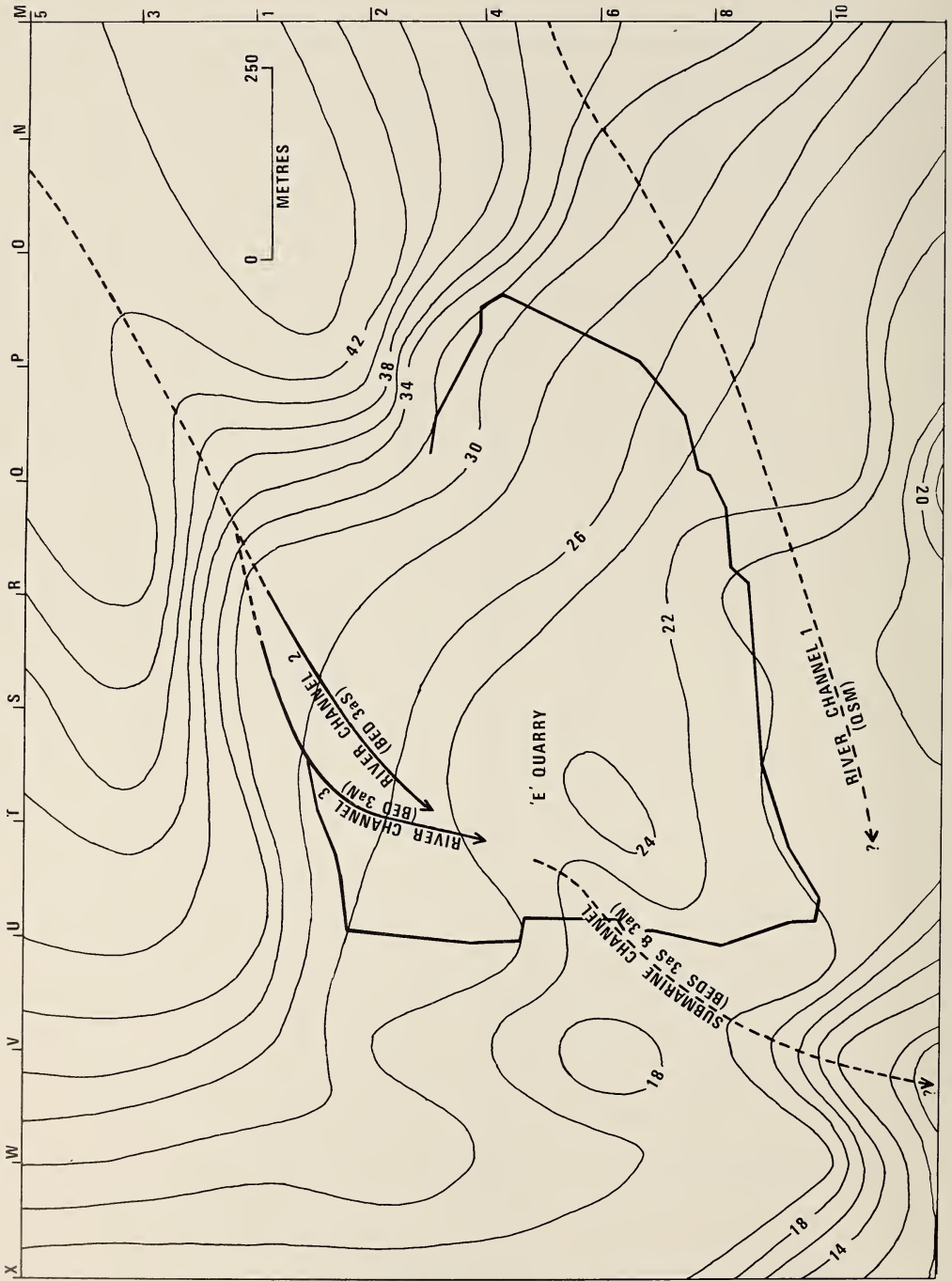
Fig. 6. Structure contour map of the base of the Pelletal Phosphorite Member (PPM). Arrowed lines indicate inferred positions of the river channels and a submarine channel at the times when the Quartzose Sand Member (QSM). PPM 3aS. and PPM 3aN were laid down. (Adapted from Tankard 1974a. Fig. 3.)

While the bed 3aS deposits overlie and are generally at a higher elevation than those of the QSM, the situation in respect of bed 3aN relative to bed 3aS is more equivocal. Some of the bed 3aN deposits are higher than any of bed 3aS, but nowhere was the former clearly superimposed on the latter. In fact, there was a lateral (westerly) truncation of bed 3aS by bed 3aN, and both were superimposed on the QSM (Fig. 6, Table 8).

The actual elevation of sea-level when the river was in its various positions cannot be accurately determined. The fossiliferous deposits of the QSM and PPM range between elevations of 30 m and 40 m, which is a possible indication of the magnitude of the sea-level rise which took place during their deposition. However, the actual rise might have been less, since much of the deposition associated with the 3aS and 3aN channels apparently took place during floods when river levels were high. Not even the elevation of the QSM tidal mudflat bed (QSM I—Table 3) is of assistance in resolving this issue, partly because this bed was truncated by overlying deposits, and partly because nothing is known of the local tidal range at that time. This range may have been large because of the estuarine situation of the mud-flat bed. The complex nature of tides in estuaries is well known, with ranges being markedly affected by the volume and strength of the river flow. In addition, it is possible that at the time that the QSM was laid down, the sea connection between the present Saldanha and St Helena Bays was incomplete, in which case the ancient Berg River, with its seasonal floods, would have discharged into a large bay, a combination of circumstances which can also affect tidal ranges.

The QSM

The first of the three positions of the river channel was not exposed in 'E' Quarry, although it is possible that some of the deposits in the south and south-east of the quarry were laid down in an enlarged flood-season channel. The proximity of the channel to this area is indicated by the nature of the deposits in the south-central part of the quarry, and, to a lesser extent, by other exposures of the QSM on the floor of the quarry. Three main depositional environments (i.e. facies) of the QSM are recognized. All were truncated during the initial stages of the deposition of overlying deposits and their original depth and areal extent can no longer be determined. Each of the facies is characterized by distinctive sediments and fossil assemblages (Table 3).

In the south-central part of 'E' Quarry there survives the vestiges of a tidally inundated mud-flat bed (QSM III of this paper, or Layer E3 of Dingle et al. 1979). The fossil assemblage of this muddy silt includes an extensive invertebrate assemblage which was described and discussed by Kensley (1977). Vertebrate remains are rare and are comprised mostly of small bone fragments washed in from elsewhere. The most remarkable of the non-invertebrate fossils are fragments of bird egg-shell, which, like some of the invertebrates, retain traces of their original colour. The invertebrates include terrestrial, freshwater, estuarine and marine species, and comprise an assemblage typical of a mud-flat environment (Kensley 1977).
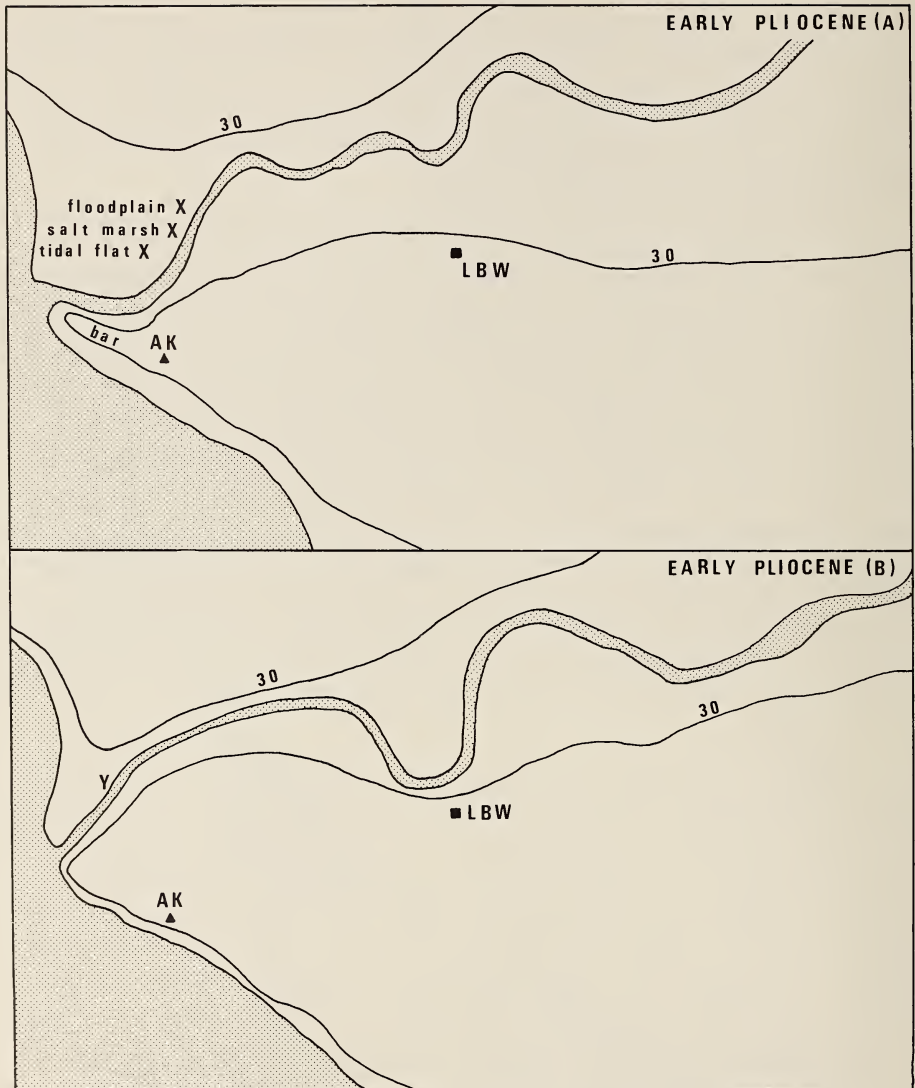
Fig. 7. The Langebaanweg area during the early Pliocene (sea-level cycle TP1). A. Period of deposition of the QSM (X-'E' Quarry exposures of the QSM). B. Period of deposition of the PPM 3aN (Y-'E' Quarry exposures of the PPM 3aN). (See Fig. 4 for key.)

Immediately adjacent to the mud-flats bed, largely in a north-easterly direction, is the more extensive 'peat' bed of the QSM (QSM II of this paper, or Layer E2 of Dingle *et al.* 1979). These black, carbonaceous sands and clays represent a marsh deposit. Their fossil content has yet to be analysed in detail, but they are rich in both pollens and vertebrate fossils. They were briefly discussed by Hendey (1976*a*: 225–226) and Rich (1980).

Elsewhere to the north-west, north, north-east, and east are exposures of the quartzose sands which are the main component of the QSM (QSM I of this paper, or Layer E1 of Dingle *et al.* 1979). These deposits apparently accumulated on the floodplain of the river, and were therefore partly subaerially and partly subaqueously deposited (Hendey 1974*a*: 32–33, 35–36, 349–353; 1976*a*: 223–224). It is believed that the inundation of these deposits during flood periods was gentle rather than torrential. In other words, the area was not affected by the strong currents in, and immediately adjacent to, the main river channel, but was inundated by slow-moving backwaters which overflowed from the main channel.

The representation of fossils in QSM I is variable both in terms of condition of specimens and associations of taxa. Apart from indicating the subaerial and subaqueous conditions of dry and wet seasons respectively, they suggest the existence of such microenvironments as ponds and minor drainage channels (Hendey 1976*a*: 223, 226). Terrestrial vertebrates predominate, and there is good evidence that at least some, and perhaps even most, were subaerially accumulated (Hendey 1974*a*: 351; 1976*a*: 224). On the other hand, some subaqueous deposition also took place, together with subaqueous disturbance of previously deposited materials. This would account for the occasional presence of aquatic species in association with terrestrial ones, and the nature of certain of the occurrences.

Although a wide variety of taxa are represented in QSM I, the most characteristic are a tortoise (*Chersina* sp.), a francolin (gen. and sp. not determined), a rhinoceros (*Ceratotherium praecox*), a pig (*Nyanzachoerus* cf. *pattersoni* (or *kanamensis*)), and a boselaphine antelope (*Mesembriportax* (or *Miotragocerus*) *acrae*). The tortoise is the most commonly represented of these taxa. Remains of this animal were sometimes present in astonishing quantity, and they occasionally occurred where no other fossils were obvious (see p. 78).

While much of QSM I was probably deposited some distance from the main channel of the river, this was not the case with the more southerly and south-easterly exposures. Here there are areas of coarser-grained sands, as well as clayey sands, while the associated fossils differ in both condition and species representation. Amongst the species recorded from these deposits are a seal (*Homiphoca capensis*) and giraffids (*Giraffa* sp., *Sivatherium hendeyi**), which are otherwise characteristic of QSM II and the channel deposits of the PPM. The seal is known from elsewhere in QSM I, but there it is represented mainly by the remains of very young individuals, whereas in the other deposits mentioned above, sub-adults and adults predominate. The latter probably died in, or near one of, their natural habitats (i.e. the river channel), whereas the very young ones of QSM I might have been carried away from their nursery by terrestrial carnivores.

To sum up, the QSM was laid down when the river channel was largely to the south and south-east of 'E' Quarry, where it was separated from the sea by a sand-bar (Fig. 7). Remnants of a tidal mud-flat deposit laid down on the

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* Churcher (1978) suggested that *S. hendeyi* is conspecific with *S. maurusium*, but it is here regarded as sufficiently distinct to warrant separate specific status.

northern margins of the estuary are preserved, as are remnants of an imme-
diately adjacent salt marsh. Elsewhere there are deposits which were inundated
by floods during the wet season. The picture that emerges is the almost classic
one of an estuarine environment and its associated sedimentary facies. The
present Berg River estuary appropriately provides an ideal modern analogue.

Perhaps the most significant characteristic that distinguishes the QSM from
the PPM is that the former are non-phosphatic. This is simply explained by the
fact that the development of authigenic phosphate did not occur in those facies
of the QSM exposed in 'E' Quarry (i.e. floodplain, salt marsh and tidal flat).
However, there evidently was phosphate deposition in other local environments
which existed at the time that the 'E' Quarry QSM deposits were laid down.
For example, the deposits comprising the sand-bar which separated the estuary
from the sea are phosphatic (Tankard 1974a), as are those which accumulated
in the marine littoral environment. The latter environment encroached on the
'E' Quarry exposures of the QSM as the transgression progressed, and resulted
in the deposition of the PPM in this area. There was a coincident north-easterly
migration of the estuarine facies in this depositional system (i.e. the QSM).

The QSM and PPM therefore represent lithostratigraphic units, and not
chronostratigrahic units (Fig. 8), and may be termed 'magnafacies', while any
chronostratigraphic units which may yet be defined would be termed 'parva-
facies' (see Krumbein & Sloss 1963: 320, fig. 9–6). It is fortuitous that none of
the PPM deposits laid down contemporaneously with the QSM have yet been
exposed in 'E' Quarry, while the QSM counterparts of the 'E' Quarry PPM
deposits are also not exposed, and may, in fact, no longer be preserved.
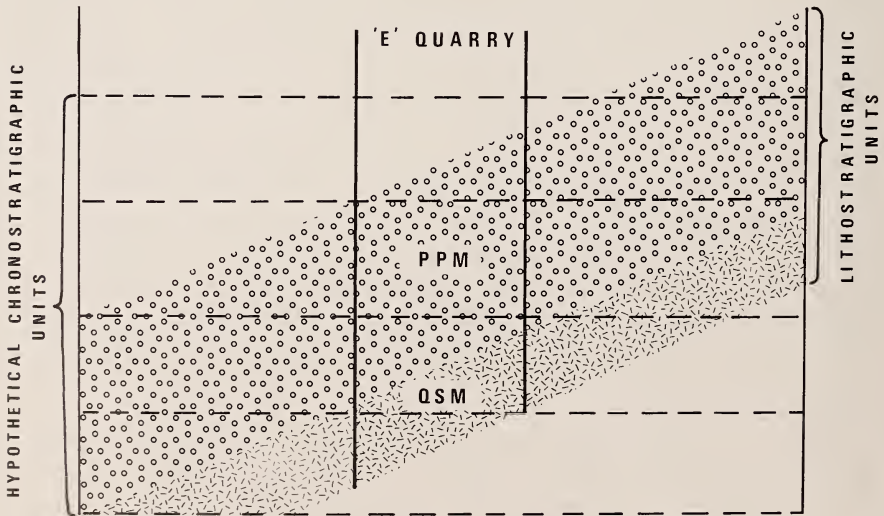

Fig. 8. A diagrammatic representation of the QSM and PPM lithostratigraphic units ('magna-
facies'), and their relationship to hypothetical chronostratigraphic units ('parvafacies').

The PPM

The channel deposits, and incorporated fossil assemblages, of beds 3aS and 3aN of the PPM are essentially similar. However, bed 3aS was in the form of a relatively straight channel superimposed on an unconsolidated substratum, whereas in the bed 3aN area an outcrop of phosphatic rock caused a southward deflection in the course of the river, and, at least in flood times, it provided a consolidated substratum for part of the channel (Hendey 1980: 58–62, fig. 26). In addition, the seaward end of bed 3aS was truncated by the bed 3aN channel. (Fig. 6), which resulted in the loss from bed 3aS of the marsh and pond facies evident in bed 3aN (Table 3).

The bed 3aN deposits were recently discussed in some detail (Hendey 1980: 58–67), and were also mentioned earlier (Hendey 1976a: 228–230). The latter account also deals with bed 3aS, while this bed (formerly 3a) was also discussed by Hendey (1974a: 33, 36–37, 353).

While beds 3aS and 3aN have many species in common with the QSM, their faunas are also in some respects distinct (see pp. 45–53), and the condition of specimens and relative numbers of individuals in any given taxon may be very different. The most characteristic of the beds 3aS and 3aN taxa are the seal (*Homiphoca capensis*), giraffids (*Giraffa* sp., *Sivatherium hendeyi*), alcelaphine antelope (*Damalacra neanica* and *D. acalla*), and a reduncine (*Kobus subdolus*). There are, however, differences in the relative numbers of individuals represented in beds 3aS and 3aN, and to a lesser extent also in the taxa represented. For example, the alcelaphines occur much more commonly than giraffids in bed 3aS, whereas in bed 3aN the reverse applies. In addition, species of *Palaeotragus*, *Tragelaphus*, and *Kobus* are known only from bed 3aN.

Most of the fossils from beds 3aS and 3aN represent the remains of animals washed into the area by the river, but at least some must represent animals that were resident locally. The latter include aquatic species such as the seal and fishes, while others might have lived on the river-banks. For example, hyaenas might have roamed the banks scavenging carcasses stranded there.

The river might have had an important effect on the composition of the bed 3aS assemblage. At the time that much of the latter was being deposited, the river was flowing over the unconsolidated and often highly fossiliferous deposits of the QSM. It is certain that at least some, and perhaps even a great many, QSM fossils were picked up by the river and redeposited in bed 3aS. Since such derived fossils might have suffered only minimal transport, they would not necessarily show obvious signs of reworking. There is little likelihood of a similarly serious complication with the bed 3aN assemblage (Hendey 1976a: 230).

Although the deposits and faunas of the QSM, bed 3aS, and bed 3aN differ, and despite the evidence that intervals of time elapsed between their deposition, there can be little doubt that they date from a relatively short period and represent repetitive depositional phases of a single geological episode. The period was long enough for evolutionary changes to take place in

taxa common to more than one level (see p. 24), and it is possible that the composition of the local fauna also changed during this time (see p. 86). However, most of the faunal differences, and all of the geological ones, can be ascribed to the exposure in various areas and levels of differing depositional environments within a major depositional system (i.e. an estuary and associated environments).

Fossils do occur in the PPM deposits overlying bed 3aN, but they are not common and probably represent the remains of animals occasionally washed into a marine littoral environment by currents emanating from the river mouth, which was progressively further from the 'E' Quarry area as the early Pliocene transgression advanced.

The upper levels of the PPM, and, indeed, all the undifferentiated parts of this unit, include marine microfossils such as foraminifera, fish teeth, and mollusc fragments (Tankard 1974a).

The record of deposition of the PPM in the Langebaanweg area is probably incomplete, since there was evidently truncation of the higher levels during the subsequent late Pliocene regression.

Mobilization of phosphate in the PPM and its redeposition into phosphatic rock horizons might have continued after deposition of the PPM itself ceased. There are several phosphatic rock horizons in the more northerly exposures of the PPM in 'E' Quarry and it is evident that they did not form contemporaneously (Dingle *et al*. 1979: 89). The one that affected distribution of bed 3aN was formed after the accumulation of the QSM and before deposition of bed 3aN, while others higher in the sequence were formed subsequently. A possibly significant feature of these horizons is that they occur only in the more northerly exposures of the PPM. The bulk of the PPM deposits, which are spread out south and south-west from 'E' Quarry, have at most thin lenses of phosphatic rock which are superficially very different in appearance. The more northerly phosphatic rock horizons cannot have formed in a deep-water continental shelf situation, which was suggested in the case of the middle Miocene phosphatic rock (see p. 20). The fact that they occur only on what was the landward side of the developing Varswater Formation, suggests the possibility that seasonal movement of the watertable in the phosphate-rich sediments might have led to precipitation of a phosphatic matrix in the zone of movement.

Deposition of pelletal phosphorite apparently ceased during a stage in the transgression when the Langebaanweg area was so deeply covered by the sea that conditions necessary for its formation were no longer being met (see Birch 1977, fig. 4).

The Anyskop marine deposits

It was previously assumed that all those deposits overlying the PPM in the vicinity of 'E' Quarry were deposited subaerially during the Quaternary (e.g. Hendey 1974a; Tankard 1974a; Bishop 1980). However, this apparently applies to only part of the overlying succession.

Although pelletal phosphorite continued to accumulate at higher eleva-
tions south-east of Langebaanweg (e.g. Elandsfontein—Rogers 1980) during
the latter stages of the early Pliocene transgression (i.e. in the shallower water
close to the river mouth and shoreline), in the immediate vicinity of Lange-
baanweg only non-phosphatic deposits were being laid down. This conclusion is
based on a reassessment of the calcareous deposits making up the bulk of
Anyskop, the hill immediately south of 'E' Quarry. These deposits have been
included in the 'Langebaan Limestone' (Visser & Schoch 1973), which Tankard
(1976) defined as a member of the Bredasdorp Formation. The 'Langebaan
Limestone' is generally regarded as a composite 'of limestone types of . . . aeo-
lian origin' (Tankard 1976: 114). The continued recognition of this lithostrati-
graphic unit is open to question, since it is evident that limestones and calcretes
of different ages and origin are included in it. The Anyskop calcareous deposits
are a case in point. The reinterpretation of these deposits which is outlined
below is tentative, and, although it may well be modified in future studies, it is
obvious that previous interpretations are incorrect.

Anyskop is a prominent feature in the Langebaanweg area, rising to an
elevation of over 70 m, while the mean elevation in the immediate vicinity is
probably about 30 m. Deposits on its northern slope have been exposed by
overburden stripping associated with the 'E' Quarry mining operation. Features
of these deposits, including a previously unknown fossil content, have been
revealed by three years (1977–1980) of subaerial weathering and erosion which
took place while mining operations were suspended. The hill itself is a curious
feature, since it may be the only one in a wide area around Langebaanweg
which does not have a core of Cape granite. In fact, the bedrock beneath the
hill is at about 35 m below sea-level (Rogers 1980), a situation which apparently
applies within a radius of several kilometres. The existence of the hill, there-
fore, has no direct connection with the solid geology of the area.

Also anomalous is the fossil content of the calcareous deposits comprising
much of Anyskop. According to Tankard (1974a: 280–281), foraminifera are
abundant, with *Anomalina* tests outnumbering those of *Elphidium* 5 : 1, the
former being 'essentially fresh', while the latter are weathered. Tankard's belief
that the forams were 'blown inland subsequent to the regression of the sea
responsible for the Varswater Formation' is inconsistent with the condition of
the *Anomalina* tests and the fact that this genus occurs most commonly in
continental shelf rather than beach situations (R. A. Martin, pers. comm.). It is
much more likely that the fresh *Anomalina* specimens were deposited in a
marine environment where no abrasion by wind or wave action was possible.
On the other hand, *Elphidium* is common in inshore situations and the abraded
conditions of the Anyskop specimens suggest that they might have been
exposed to the wind or waves. It is probably also significant that, whereas
Elphidium and other inshore forams are recorded from the underlying marine
littoral PPM, *Anomalina* is not.

One possible interpretation of the above observations is that the calcareous

deposits of Anyskop were in part accumulated in a marine environment of deeper water than the PPM, and also in part on a beach or adjacent terrestrial environment. This is a combination of circumstances which exists on a sub-merged barrier or barrier island. It is perhaps significant that the south-east to north-west trend of Anyskop parallels at least a part of the sand-bar which existed in QSM and PPM times, and it is conceivable that a submerged barrier or barrier island was a vertical and north-eastward development from this sand-bar as the Pliocene transgression progressed. Figure 9 illustrates the hypothetical submerged barrier or barrier island in a 'drumstick' form of the kind described for such features by Hayes (1976). The most substantial part of this 'drumstick' survives as Anyskop today. The east–west trend of the barrier (Fig. 9) is conjectural, and it might instead have extended southwards towards Karnberg (Fig. 2; see also p. 39).

The development of this barrier was a very significant event, since the deposits constituting it were subsequently to protect from erosion the underlying and northward-extending Varswater Formation that survives today. The preservation of so substantial a body of unconsolidated late Tertiary sediment has hitherto been difficult to explain, just as there was no obvious reason why Anyskop should have been developed by aeolian action in its present position and form.

An apparent anomaly with this interpretation is the observation by Tankard (1974a) that the most commonly occurring fossils in the calcareous sands are shells of the land snail, *Trigonephrus globulus*. Also common are shells of
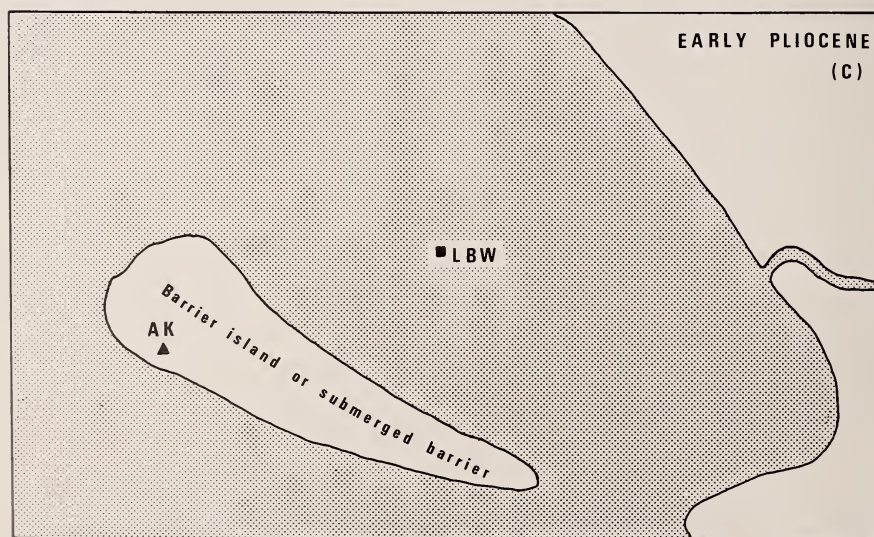
Fig. 9. The Langebaanweg area during the early Pliocene (sea-level cycle TP1). C. Period of deposition of the Anyskop marine deposits. Sea-level at about 60 m above present level (transgression maximum at 90 m). (See Fig. 4 for key.)

another, unidentified land snail. The snail shells are now known to occur together with fragmentary vertebrate remains, mainly of terrestrial species, although marine and freshwater taxa are also recorded. Associated with these fossils are 'fossil roots' (rhizoconcretions) and as yet unexplained circular structures of calcrete with infillings of reddish sands (Fig. 10). The latter have been suggested to represent remnants of tree stumps or clumps of sedge, termitaria, or solution cavities.
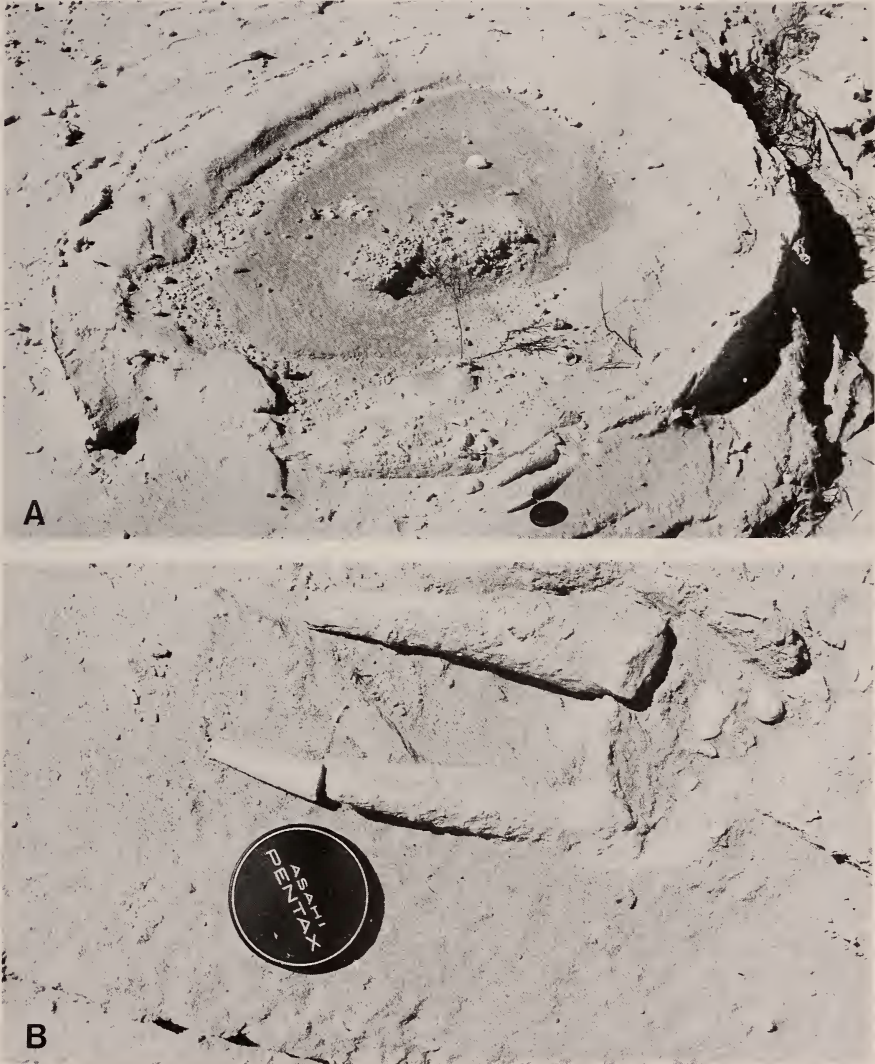
Fig. 10. A. An exposure of the Anyskop terrestrial deposits showing one of the unidentified features referred to in the text, together with snail shells and the horn-cores of an unidentified antelope. B. A close-up view of a snail shell and the antelope horn-cores.

There can be little doubt that these structures, the rhizoconcretions, and the fossils mark an old land surface. They appear to be confined to a horizon extending from high up the north slope of Anyskop down towards the 'E' Quarry exposures of the PPM, although they are not known to occur *in situ* below an elevation of about 40–45 m. In areas on the north slope which have been excavated well below the present surface, the structures and fossils are absent. These observations suggest that the old land surface was more or less coincident with the present northern contours of Anyskop, occurring over a limited vertical extent of the calcareous deposits immediately beneath the unconsolidated surface sands. In other words, the fossils were deposited *on* Anyskop at a time when the north slope was more or less in its present form.

The vertebrate fossil assemblage is as yet unstudied, and it may be too small and the fossils too fragmentary to give an accurate indication of age. The assemblage is, however, definitely distinct from those of the underlying QSM and PPM. It includes at least one species otherwise known only from the late Pliocene/early Pleistocene Baard's Quarry assemblage (i.e. *Hipparion baardi*, an advanced member of the lineage which includes the 'E' Quarry *H*. cf. *baardi*—Hooijer 1976; Hendey 1978*a*). On the other hand, an unidentified antelope from the Anyskop fauna (Fig. 10) is clearly distinct from the ones represented at Baard's Quarry, and, indeed, all other antelopes hitherto recorded from the south-western Cape.

The implications of the Anyskop ancient land surface will be discussed below, but its significance here is that there appears to be no direct association between its terrestrial fossils and the marine fauna (including forams) recorded by Tankard (1974*a*). Consequently, a distinction is made between the 'Anyskop marine deposits' and the 'Anyskop terrestrial deposits', with the former being correlated with the early Pliocene transgression, and the latter post-dating this event. There is an as yet undetermined relationship between the Anyskop deposits and those overlying the Varswater Formation on the western side of 'E' Quarry (exposure 1 of Dingle *et al*. 1979, figs 2–3).

The early Pliocene transgression reached an elevation of 90 m, which is about 20 m above the maximum height of Anyskop. While it is possible that post-early Pliocene erosion reduced the height of Anyskop, it might never have been as high as 90 m, which means that at least during the latter stages of the transgression, Anyskop was probably in the form of a submerged barrier rather than a barrier island.

Remnants of the 90 m marine platform exist to the south-east of Langebaanweg. Its presence is inferred from the topography (Mabbutt 1956), while marine deposits up to an elevation of 80 m have been recorded on the farm Elandsfontein (Rogers 1980). Evidently it was developed in the lee of a series of hills formed by outcrops of Cape granite. The trend of these hills is from north-west to south-east, roughly parallel to the present coast. The hills are Karnberg (177 m), 12 km south-south-west of Langebaanweg, followed by Massenberg (161 m), Groot Swartberg (287 m), and Slangkop (258 m). Subse-

quent to its formation the 90 m platform was incised by the valley of the Sout River, a northward-flowing tributary of the Berg River (Fig. 2).

It was suggested above that the Anyskop barrier island may have extended southwards in the direction of Karnberg, rather than eastwards as indicated in Figure 9. If this was indeed the case, then Karnberg and the other hills in the series must have been influencing the local topography at an earlier stage during the early Pliocene transgression. The Anyskop barrier island might in fact, have been a longshore spit extending northwards from Karnberg.

This, and other, uncertainties relating to the later history of the early Pliocene transgression should be resolved by further investigation of relevant deposits in the Langebaanweg area.

The early Pliocene transgression which resulted in deposition of the QSM, PPM, the Anyskop marine deposits and other marine deposits south-east of Langebaanweg, represents sea-level cycle TP1 of supercycle Tf (Vail & Hardenbol 1979: fig. 8).

The late Pliocene regression and early Pleistocene transgression

The history of late Pliocene and early Pleistocene deposition in the Langebaanweg area is as yet not well documented, and inference played a large part in the interpretation outlined below, with the nature and likely age of the Anyskop terrestrial deposits and Baard's Quarry fluviatile deposits being of particular significance in this interpretation.

It is unlikely that Anyskop was in its present form during the early stages of the late Pliocene regression. Had this been the case then it would have been in the form of an island a few kilometres off the emergent mainland. The fact that a vertebrate fauna, which is correlated with an early stage of the regression, left traces of its presence on the north slope of Anyskop when the sea was at an elevation of between 40 and 60 m, means that a connection with the mainland must have existed. This connection probably followed the trend of the pre-existing coastal barrier, which might have been north–south, rather than east–west, as indicated in Figure 11.

Figure 11 also shows the ancient Berg River passing westwards along the northern side of this connection and meeting the sea to the south-west of 'E' Quarry. There is, in fact, no direct evidence for the position of the river, while its local presence is inferred simply because it is the most likely source of fresh water required by species such as the hippopotamus in the Anyskop fauna. A more tenuous indication that the river was present locally is the unequivocal evidence for its presence both during the early Pliocene (see above) and subsequently during the late Pliocene/early Pleistocene (see below).

A sea-level elevation of about 50 m at this time is deduced from the presence of a marine element in the Anyskop fauna, and from the recorded elevation of the Anyskop terrestrial fossils and associated features. In addition, the PPM of the Varswater Formation has been eroded down to a maximum elevation of 50–55 m in the vicinity of Anyskop. The maximum elevations for
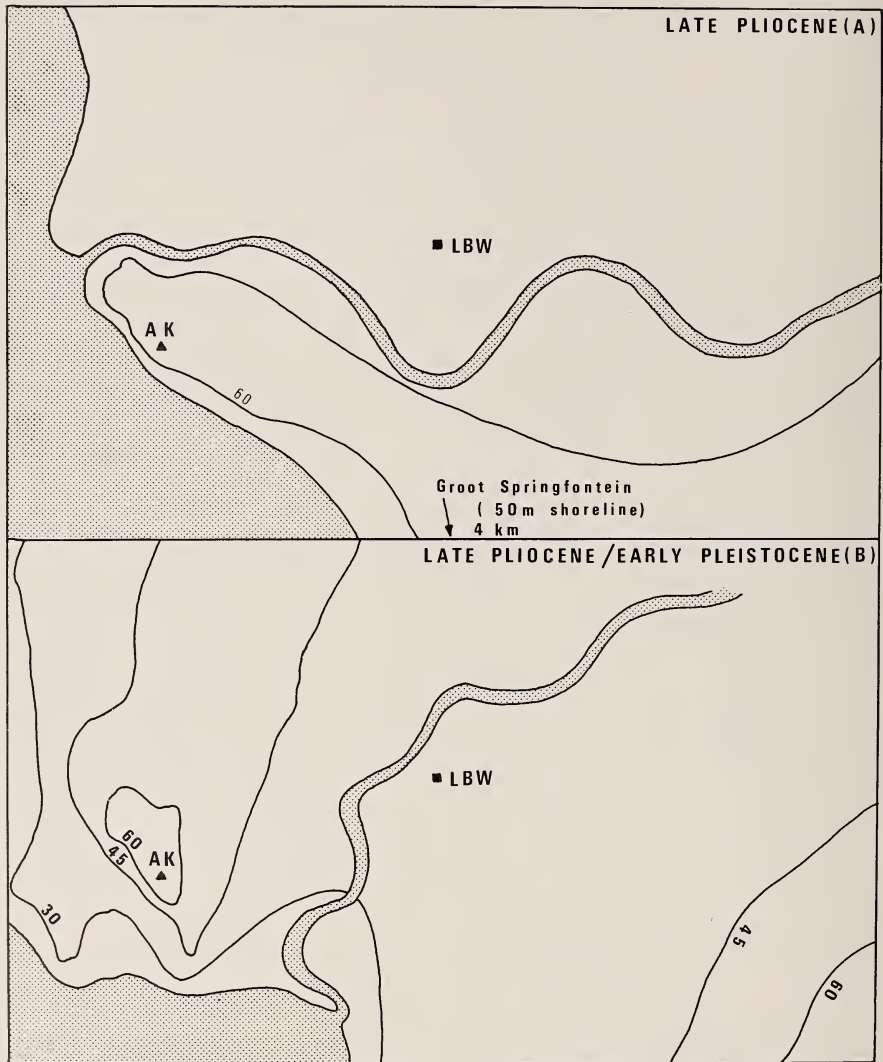
Fig. 11. The Langebaanweg area during the late Pliocene (sea-level cycle TP2) and the late Pliocene or early Pleistocene (sea-level cycle TP3 or Q1). A. Period of deposition of the Anyskop terrestrial deposits. B. Period of deposition of the Baard's Quarry fluviatile deposits. (See Fig. 4 for key.)

the PPM recorded by Tankard (1974a) are 53–54 m near 'E' Quarry, 54 m on the farm Witteklip and at Paternoster, and 47–50 m at Duiker Eiland. Tankard also records a marine horizon at 50 m on the farm Groot Springfontein, south-east of Anyskop, the nature of the deposits and associated fossils indicating a shoreline situation.

The various occurrences at about 50 m elevation are here interpreted as representing a temporary stillstand in the Pliocene regression, probably the first of two such stillstands during this event recorded by Vail & Hardenbol (1979) in their synthesis of global sea-level changes (i.e. cycle TP2 of supercycle Tf).

Slender though the evidence may be, the vertebrate fauna of the Anyskop terrestrial deposits suggests an age close to, but not necessarily contemporaneous with, the fauna from the Baard's Quarry fluviatile deposits (i.e. late Pliocene/early Pleistocene). It is, therefore, not inconsistent with the inferred Pliocene age of the 50 m shoreline.

As indicated above, there is unequivocal evidence for the presence of the river during the late Pliocene/early Pleistocene. This is in the form of channel deposits revealed west of Langebaanweg station by the prospecting for, and mining of, phosphate (Tankard 1974a; Hendey 1978a). They are here referred to as the 'Baard's Quarry fluviatile deposits', and are correlated with the west coast 20 m shoreline. This represents either the second of the stillstands in the Pliocene regression recorded by Vail & Hardenbol (1979) (i.e.cycle TP3 of supercycle Tf), or the climax of the early Pleistocene transgression (i.e. cycle Q1 of supercycle Q).

According to Vail & Hardenbol (1979, fig. 8) cycle TP3 spanned the period between 3,8 and 2,8 Ma, the latter being taken by them as the Pliocene–Pleistocene boundary, while cycle Q1 is dated between 2,8 and 1,7 Ma. The mammalian fauna of the Baard's Quarry fluviatile deposits (= 'lower levels' fauna of Hendey 1978a) also suggested an age close to the Pliocene–Pleistocene boundary, and it has recently become evident that at least one element in this fauna is unlikely to be older than 1,9 Ma (see p. 95). Consequently, the Baard's Quarry fluviatile deposits are more likely to date from cycle Q1 than cycle TP3. This is consistent with the record of the cold-water fauna associated with the counterpart of the Baard's Quarry fluviatile deposits on the Namaqualand coast (Table 2; see also p. 16), and the suggestion that cold-water faunas are characteristic of the Quaternary.

Figure 11 shows the river meeting the sea south-east of Anyskop, with the pre-existing barrier island link to the mainland having been severed. If this link did exist, then it is most likely to have been destroyed by river erosion. the coincidence of this event with the 20 m stillstand is suggested by the fact that the Baard's Quarry fluviatile deposits are situated on a broad, flat plain (? an ancient floodplain), which extends southwards through the area where the hypothetical Anyskop-'mainland' connection existed (Fig. 11). It would have been at this time that Anyskop took on its present form.

Subsequently, the river underwent a radical change in direction in its lower course, shifting northwards to begin incising its present valley in the direction of St Helena Bay. This process continued during the Pleistocene and at least by the beginning of the late Pleistocene the Berg River must have been more or less in its present position, since Tankard (1976) has identified last interglacial marine deposits in the existing valley.

Once the river and the sea were no longer in the vicinity of Langebaanweg, sedimentation in the area was insignificant. The minor events of the Quaternary included the development of the unconsolidated aeolian sands which blanket the area, and duricrust (mainly calcrete) formation within them and in underlying deposits. Early Stone Age artefacts, probably of middle Pleistocene age, have been found cemented into the calcrete immediately underlying the surface sands on Anyskop, and there is evidence for post-middle Pleistocene human occupations in the area as well. There are recorded vertebrate fossil occurrences dating from the ?early Pleistocene (Skurwerug, near Saldanha), middle Pleistocene (Elandsfontein), and late Pleistocene (Sea Harvest at Saldanha, and others).

The late Cenozoic sequence in the Langebaanweg area is in many respects unique, and although much attention has been focused on it, especially during the last decade, most of the geological studies (e.g. Butzer 1973; Visser & Schoch 1973; Tankard 1974a; Bishop 1980) have dealt only superficially with the fossil occurrences and the nature of the various depositional environments represented. Consequently, there is still a need for further study directed specifically at the context of the recorded fossil assemblages and the history of the deposits, especially those post-dating the PPM of the Varswater Formation. Since large volumes of deposit have been mined away, it is no longer possible to retrieve all the information on the succession which was once available. Nevertheless, documentary records, sediment samples and exposures still exist, and they offer a potential for further research.

BIOLOGY

FLORA

The flora of the Langebaanweg area during the period of deposition of the late Cenozoic succession is not well known. Initially only indirect evidence was available from which the nature of the local vegetation during QSM and PPM times could be deduced. For example, large browsers amongst the herbivores, particularly the long-necked giraffe (*Giraffa* sp.), have been cited on several occasions as indicating the presence of trees (e.g. Hendey 1973, 1974a, 1976a, 1980). On the other hand, hypsodont grazing species such as the rhinoceros (*Ceratotherium praecox*) indicate that grasslands were also present. The possible significance of the relative abundance of browsers and grazers at different levels within the Varswater Formation will be discussed later (see p. 75).

Other indirect evidence for the presence of plants was that of leaf impressions, probably of grass or reeds, on coprolites from the QSM (Hendey 1976a: 224). Attempts to recover pollens from coprolites have so far proved fruitless.

Physical remains of plants themselves are limited to pollens, algal nucules, and fragments of petrified roots. Studies on pollens from the 'peats' of the Varswater Formation and underlying deposits have yet to be published, but passing references to these pollens have been made by Tankard (1975b), Hendey (1976a), Tankard & Rogers (1978), and Dingle *et al.* (1979). In

addition, although not specifically mentioned, the pollens contributed to Coetzee's (1978) study on vegetational changes in the south-western Cape during the late Tertiary. These pollens indicate that the local vegetation during pre-GM times (i.e. Miocene) was dominated by forests and woodlands, whereas by QSM times (i.e. early Pliocene) sclerophyll (fynbos) vegetation was becoming prominent. Details of the Langebaanweg pollen record will be published elsewhere (J. A. Coetzee, in preparation).

The algal nucules (charophytes) were identified and discussed by Kensley (1977), and they have also been studied by I. Soulié (Montpellier), although her report on them is as yet unpublished. They were preserved in the tidal flat bed of the QSM (i.e. QSM III), and were probably derived from freshwater ponds on the QSM floodplain (i.e. QSM I). The existence of such ponds was postulated by Hendey (1976a).

The fossil roots, which are in the form of slender fragments mostly from the QSM, have not been studied. It is unlikely that they will reveal much about the plants to which they belonged.

In conclusion, it should be mentioned that the rhizoconcretions and the unidentified structures of the Anyskop terrestrial deposits may provide some indication of the local vegetation later in the Pliocene.

FAUNA

Composition

This section deals only with the fauna of the Varswater Formation, from which the assemblage of invertebrate and vertebrate fossils is exceptionally large, both in terms of the numbers of specimens and in the variety of species represented. However, it represents only a small fraction of the material which was preserved in the deposits, much of which was lost during mining operations and much of which remains unexcavated.

At least 230 distinct taxa have been recognized, ranging from protozoans to mammals. Vertebrates predominate, and there are many phyla of lower animals that are not recorded. Important groups such as the insects are also lacking, the only tangible evidence of their presence being grooves on bovid horn-cores left by keratophagous insect larvae (Fig. 12). Most specimens are well preserved and individual species assemblages range from a few to many thousands of specimens. Most taxa are identifiable to species level, and incomplete identifications usually indicate that taxonomic studies have yet to be undertaken.

The list of taxa which follows is given in systematic order and according to the horizon from which material was derived. Material of doubtful provenance (?) is listed under horizons where its presence was likely. In the case of the equid, *Hipparion* cf. *namaquense*, it is still not known if the relevant material came from the uppermost levels of the PPM, or the lowermost levels of the overlying deposits (Hooijer 1976). Inferred habitat preferences are given, and in instances where resting and feeding habitats differ (e.g. amongst many birds), the latter are recorded.
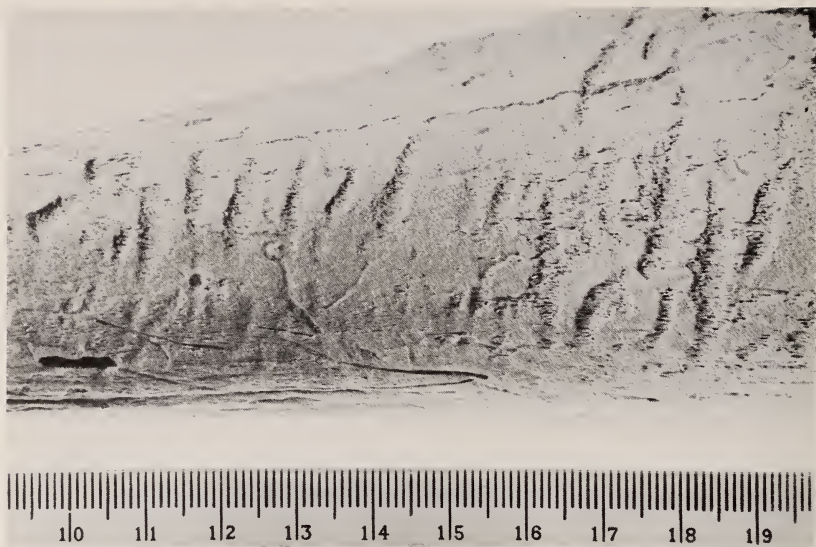
Fig 12.   Marks left on a *Mesembriportax acrae* horn-core from the PPM 3aS
(SAM–PQ–40071) by keratophagous insect larvae.

Although the lists for individual horizons broadly reflect the local fauna of the period of deposition, they do not necessarily represent the fauna of a single habitat. In the case of some levels it is possible that the assemblages include specimens derived from pre-existing deposits. This applies particularly in the case of the fluviatile deposits (beds 3aS and 3aN), which are, in addition, comprised largely of taxa whose remains were washed into the area from upstream habitats. Palaeoecological interpretations of the assemblages constituting the 'E' Quarry fauna must, therefore, take these factors into account.

An example of the palaeoecological studies which are possible is that by Kensley (1977) on the invertebrate assemblage from QSM III (i.e. the tidal-flat bed). In this instance the remains of the resident animal community were supplemented by others washed downstream by the river and upstream by the tides. This assemblage proved to be essentially similar to ones in comparable situations today, and, interestingly, it proved a better indication of the nature of the depositional environment than the sediments themselves.

This was a general rule with most 'E' Quarry sediments, and attempts to interpret their history without taking into account the composition of individual assemblages and the condition of specimens, resulted in mistaken conclusions. For example, Butzer (1973) misinterpreted the depositional environments of the QSM (= Bed 2) and bed 3aS (= bed 3a) through using only geological evidence. While Bishop (1980) evidently appreciated the significance of the fossils, he supported Butzer's conclusions and ignored the palaeontological evidence which became available after 1970.

	GM	QSM	PPM 3aS	PPM 3aN	PPM undiff.	Inferred habitat preference
PHYLUM PROTOZOA						
ORDER FORAMINIFERA						
Ammonia beccarii . .	—	—	—	—	×	marine (littoral) and
Elphidium advenum . .	—	—	—	—	×	estuarine
Cibicides lobatulus . .	—	—	—	—	×	marine (littoral;
Planorbulina mediterranensis	—	—	—	—	×	attached to vegetation
Rosalina cf. *bradyi* . .	—	—	—	—	×	etc.)
PHYLUM BRACHIOPODA (lamp shells)						
Kraussina rubra . . .	×	—	—	—	—	marine (rocky shore)
PHYLUM ECHINODERMATA						
CLASS ECHINOIDEA (sea urchins)						
Parechinus angulosus . .	×	—	—	—	—	marine (rocky shore)
PHYLUM ARTHROPODA						
CLASS CRUSTACEA						
ORDER CIRRIPEDIA (acorn barnacles)						
Gen. and sp. indet. . .	×	—	—	—	—	marine (rocky shore)
? ORDER DECAPODA (lobsters etc.)						
Gen. and sp. indet. . .	×	—	—	—	—	marine, estuarine and fresh water
SUBCLASS OSTRACODA						
Family Cytheridae						
Gomphocythere expansa . .	—	×	—	—	—	
Family Cyprididae						
Zonocypris cordata . .	—	×	—	—	—	fresh water
Family not det.						
Gen. and at least 3 spp not det.	—	×	—	—	—	
PHYLUM MOLLUSCA						
CLASS GASTROPODA						
ORDER ARCHAEOGASTROPODA						
Family **Patellidae** (limpets)						
Cellana capensis . . .	×	—	—	—	—	marine (rocky shore, warm water)
? *Cellana* sp. . . .	×	—	—	—	—	marine (rocky shore)
Patella granularis . .	×	—	—	—	—	
Family **Fissurellidae** (keyhole limpets)						
Diodora parviforata . .	×	—	—	—	—	marine (rocky shore)
Family **Haliotidae** (perlemoens or abalones)						
*Haliotis saldanhae . .	×	—	—	—	—	marine (rocky shore)
Haliotis sp. . . .	×	—	—	—	—	
Family **Trochidae** (top shells)						
Oxystele tigrina . . .	×	—	—	—	—	
Oxystele variegata . .	—	×	—	—	—	marine (rocky shore)
Gibbula benzi . .	—	×.	—	—	—	
Family **Turbinidae** (turban shells)						
Turbo sarmaticus . .	×	—	—	—	—	marine (rocky shore, warm water)
Family **Phasianellidae** (pheasant shells)						
Tricolia neritina . . .	×	×	—	—	—	marine (rocky shore)
Tricolia capensis . . .	—	×	—	—	—	marine (rocky shore, cold water)
ORDER MESOGASTROPODA						
Family **Littorinidae** (periwinkles)						
Littorina cf. *knysnaensis* .	—	×	—	—	—	marine (rocky shore)
? *Littorina* sp. . . .	×	—	—	—	—	

	GM	QSM	PPM 3aS	PPM 3aN	PPM undiff.	Inferred habitat preference
Family Hydrobiidae (snails)						
Tomichia ventricosa	—	×	—	—	—	fresh or brack water
Family Assimineidae (snails)						
Assiminea sp.	—	×	—	—	—	mainly estuarine
ORDER NEOGASTROPODA						
Family Muricidae (rock shells or whelks)						
Ocenebra scrobiculata	×	—	—	—	—	marine (rocky shore)
Family Thaisidae (rock shells or whelks)						
Thais dubia	×	—	—	—	—	marine (rocky shore)
Family Columbellidae (dove shells)						
Pyrene albuginosa	—	×	—	—	—	marine (rocky shore, warm water)
Family Nassariidae (plough shells, dog whelks)						
Bullia sp.	×	—	—	—	—	marine and/or estuarine
Bullia digitalis	—	×	—	—	—	marine (sandy shore)
Bullia laevissima	—	×	—	—	—	marine (sandy shore) and estuarine
Bullia sp. nov.	—	×	—	—	—	marine and/or estuarine
Nassarius cf. *analogicus*	—	×	—	—	—	marine (sandy shore) and estuarine
Nassarius sp. B	—	×	—	—	—	marine and/or estuarine
Nassarius sp. C	—	×	—	—	—	marine and/or estuarine
Family Marginellidae						
Marginella sp.	—	×	—	—	—	marine and/or estuarine
Family Turridae (screw shells)						
'Crassispira' sp.	×	—	—	—	—	} marine
'Clavatula' sp.	×	—	—	—	—	
'Turris' sp.	×	—	—	—	—	
ORDER ENTOMOTAENIATA						
Family Pyramidellidae						
Turbonilla kraussi	×	—	—	—	—	} marine
? *Pyramidella* sp.	×	—	—	—	—	
ORDER BASOMMATOPHORA						
Family Siphonariidae (false limpets)						
Siphonaria sp.	×	—	—	—	—	marine (rocky shore)
Family **Ferrissiidae** (snails)						
Burnupia capensis	—	×	—	—	—	on rushes in fresh water or estuaries
Family Planorbidae (snails)						
Ceratophallus natalensis	—	×	—	—	—	fresh water (subtropical, tropical)
Bulinus 'tropicus'	—	×	—	—	—	fresh water
ORDER STYLOMMATOPHORA						
Family Succineidae (snails)						
Succinea sp.	—	×	—	—	—	terrestrial or semi-aquatic (fresh water)
Family **Endodontidae** (snails)						
Trachycystis cf. *capensis*	—	×	—	—	—	terrestrial

	GM	QSM	PPM 3aS	PPM 3aN	PPM undiff.	Inferred habitat preference
CLASS AMPHINEURA						
Family **Chitonidae** (chitons)						
Chiton nigrovirescens . .	—	×	—	—	—	marine (rocky shore, cold water)
CLASS PELECYPODA						
Family **Donacidae** (sand mussels)						
Donax serra . . .	cf.	×	—	—	—	} marine (sandy shore)
Donax sp(p) . . .	×	—	—	—	—	
Family **Carditidae** (false cockles)						
*Cuna aquaedulcensis . .	—	×	—	—	—	marine
Family **Arcidae** (ark shells)						
Barbatia obliquata . .	×	—	—	—	—	marine (rocky shore, warm water)
Family **Mytilidae** (mussels)						
? *Perna* sp. . . .	×	—	—	—	—	marine (rocky shore)
Family **Veneridae** (venus shells)						
Pitar sp.	×	—	—	—	—	marine
MOLLUSCA INDET. . . .	—	—	—	—	×	
PHYLUM CHORDATA						
CLASS CHONDRICHTHYES						
ORDER SELACHII (sharks)						
Family **Hexanchidae**						
Notidanus serratissimus .	×	—	—	—	—	marine
Family **Carcharhinidae**						
Carcharhinus melanopterus .	×	—	—	—	—	} marine (warm water)
Carcharhinus limbatus .	×	—	—	—	—	
Galaeorhinus sp. . .	×	—	—	—	—	
Prionace glauca . .	×	—	—	—	—	
Negaprion or *Hypoprion* sp. .	×	—	—	—	—	
Family **Odontaspidae**						
Odontaspis accutissima .	×	—	—	—	—	
Odontaspis sp. B .	×	—	—	—	—	
Odontaspis sp. C .	×	—	—	—	—	
Family **Otodontidae**						} marine
Megaselachus megalodon .	×	—	—	—	—	
Family **Carcharodontidae**						
Carcharodon sp. . .	×	—	—	—	—	
Family **Isuridae**						
Isurus sp. . . .	×	—	—	—	—	
Family **Squalidae**						
Squalus sp. . .	×	—	—	—	—	
Family **Squatinidae**						
Squatina africana .	×	—	—	—	—	marine (warm water)
Squatina sp. B . .	×	—	—	—	—	marine
SELACHII not det. . .	×	×	×	×	—	
ORDER BATOIDEA (skates, rays)						
Family **Rajidae** (skates)						
Raja sp. . . .	×	—	—	—	—	
Family **Trygonidae** (sting rays)						
Gen. and sp. not det. .	×	—	—	—	—	} marine
Family **Myliobatidae** (eagle rays)						
Myliobatis sp. . .	×	—	—	—	—	
CLASS OSTEICHTHYES						
ORDER PERCIFORMES						
Family **Sparidae** (mussel-crackers)						
Gen. and sp. not det. . .	×	—	—	—	—	marine

	GM	QSM	PPM 3aS	PPM 3aN	PPM undiff.	Inferred habitat preference
ORDER SILURIFORMES						
Family **Tachysuridae** (catfish)						
? *Tachysurus* sp. . . —		×	×	×	—	marine and estuarine
OSTEICHTHYES not det. . . ×	×	×	×	×	×	
CLASS AMPHIBIA						
ORDER ANURA (frogs, toads)						
Gen. and sp(p) not det. . —		×	×	×	—	terrestrial and fresh water
CLASS REPTILIA						
ORDER CHELONIA (tortoises, turtles)						
Chersina sp. . . . ×	×	×	×	×	—	terrestrial
Gen. and sp. not det. . . —		×	—	—	—	marine or fresh water
Gen. and sp. not det. . . —		—	—	×	—	marine or fresh water
ORDER SQUAMATA						
SUBORDER LACERTILIA						
Family **Chameleontidae** (chameleons)						
Gen. and sp(p) not det. . —		×	×	×	—	bushes and trees
Family **Gekkonidae** (geckos) .						
Gen. and sp(p) not det. . —		×	×	×	—	terrestrial
Family **Varanidae** (leguans, monitor lizards)						
Varanus sp. . . . —		×	—	—	—	terrestrial or fresh water
SUBORDER OPHIDIA (snakes)						
Gen. and sp(p) not det. . —		×	×	×	—	terrestrial
SQUAMATA not det. . . . —		×	×	×	—	
CLASS AVES						
ORDER STRUTHIONIFORMES						
Family **Struthionidae** (ostriches)						
Struthio sp. . . . —		—	×	×	—	terrestrial (open country)
ORDER SPHENISCIFORMES						
Family **Spheniscidae** (penguins)						
***Inguza predemersus* . . —		×	cf.	?	—	⎱ marine (mainly coastal,
**Dege hendeyi . . . cf.		×	?	×	—	⎰ cold water)
ORDER PODICIPEDIFORMES						
Family **Podicipedidae** (grebes)						
Gen. and sp. not det. . . —		×	—	×	—	? fresh water
ORDER PROCELLARIIFORMES (petrels etc.)						
Gen. and at least 3 spp not det. . . . . —		×	—	×	—	marine (pelagic)
ORDER PELECANIFORMES (pelicans etc.)						
Fam., gen. and sp. not det. . . —		×	—	—	—	
Family **Phalacrocoracidae** (cormorants)						
Gen. and at least 2 spp not det. . . . . —		×	—	×	—	marine and/or fresh water
? Family **Sulidae** (gannets)						
Gen. and sp. not det. . . —		×	—	—	—	marine
ORDER CICONIIFORMES						
Family **Ciconidae** (storks)						
Gen. and sp. not det. . . —		×	—	×	—	terrestrial (open country and/or marsh)

	GM	QSM	PPM 3aS	PPM 3aN	PPM undiff.	Inferred habitat preference
Family **Threskiornithidae** (ibises, spoonbills)						
Gen. and sp. not det. .	—	×	—	—	—	terrestrial (open country) and fresh water
ORDER ANSERIFORMES						
Family **Anatidae** (ducks, geese)						
Gen. and at least 4 spp not det. .	—	×	—	×	—	fresh water and estuarine
ORDER FALCONIFORMES						
Family **Falconidae** (falcons)						
Gen. and sp. not det. .	—	×	—	—	—	aerial, arboreal and/or terrestrial
Family **Accipitridae** (hawks, eagles etc.)						
Gen. and at least 4 spp not det. .	—	×	—	×	—	aerial, arboreal and/or terrestrial
? Gypaetinae (vultures) gen. and sp. not det. .	—	×	—	—	—	terrestrial (open country)
ORDER GALLIFORMES						
Family **Phasianidae** (game birds)						
Gen. and at least 2 spp (francolin and quail) not det. .	—	×	×	×	—	terrestrial (open country with low cover)
ORDER GRUIFORMES						
Family **Gruidae** (cranes)						
Gen. and sp. not det. .	—	—	—	×	—	terrestrial (open country, marsh)
Family **Rallidae** (rails)						
Gen. and sp. not det. .	—	×	—	×	—	terrestrial (dense cover) and fresh water
Family **Otidae** (bustards) .	—	×	—	—	—	terrestrial (open, mainly dry country)
ORDER CHARADRIIFORMES (shorebirds)						
Fam., gen. and at least 10 spp not det. .	—	×	—	×	—	fresh water, estuarine and/or marine
Family **Pteroclidae** (sandgrouse)						
Gen. and sp. not det. .	—	×	—	—	—	terrestrial (near water)
ORDER COLUMBIFORMES						
Family **Columbidae** (pigeons, doves)						
Gen. and at least 2 spp not det. .	—	×	—	×	—	terrestrial and arboreal
ORDER PSITTACIFORMES (parrots)						
Fam., gen. and at least 2 spp not det. .	—	×	—	?	—	arboreal (forests, woodlands)
ORDER STRIGIFORMES						
Family **Strigidae** (owls)						
Gen. and at least 2 spp not det. .	—	×	—	—	—	arboreal and terrestrial

	GM	QSM	PPM 3aS	PPM 3aN	PPM undiff.	Inferred habitat preference
ORDER COLIIFORMES						
Family **Coliidae** (colies)						
Gen. and sp. not det. . .	—	×	—	—	—	arboreal (bushland and woodland)
ORDER CORACIIFORMES (rollers etc.)						
Fam., gen. and sp. not det. . .	—	×	—	—	—	arboreal and terrestrial
? Family **Alcedinidae** (kingfishers)						
Gen. and at least 2 spp not det.	—	×	—	—	—	fresh water
ORDER PICIFORMES (woodpeckers etc.)						
Fam., gen. and at least 2 spp not det. . . .	—	×	—	—	—	arboreal and terrestrial
ORDER APODIFORMES						
Family **Apodidae** (swifts)						
Gen. and sp. not det. . .	—	—	×	—	—	aerial
ORDER PASSERIFORMES (songbirds)						
Fam., gen. and at least 9 spp not det. . . .	—	×	—	×	—	varied
AVES not det.	—	×	×	×	—	
CLASS MAMMALIA						
ORDER INSECTIVORA						
Family **Chrysochloridae** (golden moles)						
Chrysochloris sp. . .	—	×	×	×	—	fossorial
Family **Soricidae** (shrews)						
Mysorex sp. . . .	—	×	—	—	—	
Suncus sp.	—	×	—	—	—	
Soricidae gen. and sp(p) not det.	—	×	×	×	—	terrestrial
Family **Macroscelididae** (elephant shrews)						
Elephantulus sp. . .	—	×	×	×	—	
ORDER CHIROPTERA (bats)						
Family **Vespertilionidae**						
Eptesicus sp. . . .	—	×	—	—	—	aerial
ORDER PRIMATES						
Family **Cercopithecidae** (monkeys etc.)						
Gen. and sp. indet. . .	—	×	—	—	—	arboreal and terrestrial
ORDER PHOLIDOTA (pangolins)						
Phataginus sp. . . .	—	×	—	—	—	terrestrial
ORDER TUBULIDENTATA (aardvarks)						
Gen. and sp. not det. . .	—	×	—	×	—	terrestrial
ORDER CARNIVORA						
Family **Canidae** (foxes, jackals etc.)						
Gen. and sp. not det. (? aff. '*Canis*' *brevirostris*) .	—	—	×	?	—	terrestrial
Vulpes sp. (fox) . . .	—	—	×	×	—	
Family **Ursidae** (bears)						
**Agriotherium africanum* .	—	—	×	×	—	terrestrial (? woodlands)

	GM	QSM	PPM 3aS	PPM 3aN	PPM undiff.	Inferred habitat preference
Family **Mustelidae** (weasels, martens etc.)						
Plesiogulo monspessulanus (wolverine) . . .	—	×	?	—	—	terrestrial (? woodlands)
*Mellivora benfieldi (honey badger) . . .	—	—	×	×	—	terrestrial
Enhydriodon africanus (otter)	—	—	×	×	—	fresh water
Family **Phocidae** (seals)						
**Homiphoca capensis . .	cf.	×	×	×	—	marine and ? estuarine
Family **Viverridae** (mongooses etc.)						
'*Viverra*' *leakeyi* (? aff. *Civettictis*) (civet) .	—	×	—	×	—	
Viverrinae gen. and sp. not det. (? aff. *Pseudocivetta*) (civet) . . .	—	×	×	×	—	
Genetta sp. (genet) . .	—	×	—	—	—	terrestrial
Herpestes spp A, B (mongooses) . .	—	×	×	—	—	
Herpestinae spp C, D, E (mongooses) . .	—	×	—	—	—	
Herpestinae not det. . .	—	—	×	×	—	
Family **Hyaenidae** (hyaenas)						
*'Adcrocuta' australis . .	—	×	?	?	—	
*Ictitherium preforfex .	—	—	×	×	—	
*Hyaena abronia . .	—	×	×	×	—	
Hyaenictitherium namaquense	—	×	—	—	—	terrestrial
Euryboas sp. . .	—	×	×	×	—	
Hyaenidae sp. E . .	—	—	×	—	—	
Hyaenidae not det. . .	—	—	×	×	—	
Family **Felidae** (cats)						
'*Machairodus*' sp. (sabre-tooth) . . .	—	•×	—	—	—	
Homotherium sp. (sabre-tooth) . . .	—	×	×	cf.	—	
Felis sp. (wildcat-like) .	—	×	—	—	—	
Felis aff. *issiodorensis* (lynx-like)	—	×	×	×	—	terrestrial
*Felis obscura (lynx-like) .	—	—	×	—	—	
Dinofelis diastemata (false sabre-tooth) .	—	×	×	×	—	
Felidae not det. . . .	—	—	×	×	—	
CARNIVORA not det.						
Gen. and sp. not det. (Canidae or Viverridae)	—	×	—	—	—	
Gen. and sp. not det. (? Procyonidae) . .	—	×	—	—	—	
Gen. and sp. not det. (? Lutrinae) . .	—	×	—	—	—	
ORDER PROBOSCIDEA (elephants and kin)						
Family **Gomphotheriidae**						
Anancus sp. . . .	—	×	×	—	—	terrestrial (woodlands)
Family **Elephantidae**						
Mammuthus subplanifrons .	—	×	?	×	—	

	GM	QSM	PPM 3aS	PPM 3aN	PPM undiff.	Inferred habitat preference
ORDER HYRACOIDEA (hyraxes or dassies)						
Family **Procaviidae**						
Procavia cf. *antiqua*	—	×	—	?	—	terrestrial or arboreal
ORDER PERISSODACTYLA						
Family **Equidae** (horses)						
Hipparion cf. *primigenium*	×	—	—	—	—	
Hipparion cf. *baardi*	—	×	×	×	—	
Hipparion cf. *namaquense*	—	—	—	—	?	terrestrial (grasslands)
Family **Rhinocerotidae** (rhinos)						
Ceratotherium praecox	—	×	×	—	—	
ORDER ARTIODACTYLA						
Family **Tayassuidae** (peccaries)						
Pecarichoerus? (or						
Barberahyus) *africanus*	—	—	×	×	—	terrestrial
Family **Suidae** (pigs)						
Nyanzachoerus cf. *pattersoni*						
(or *kanamensis*)	—	×	—	—	—	terrestrial
Nyanzachoerus cf. *jaegeri*	—	—	×	—	—	(? woodlands)
Family **Hippopotamidae** (hippos)						
Gen. and sp. not det.	—	—	×	×	—	fresh water and terrestrial
Family **Giraffidae** (giraffes)						
Sivatherium hendeyi	—	×	×	×	—	
Palaeotragus cf. *germaini*	—	—	—	×	—	terrestrial (woodlands)
Giraffa sp.	—	×	×	×	—	
Family **Bovidae** (buffaloes, antelopes etc.)						
Tragelaphus sp. A (nyala-like)	—	×	×	×	—	
Tragelaphus sp. B (nyala-like)	—	—	—	×	—	
Mesembriportax (or *Miotragocerus*) *acrae* (kudu like relative of nilgai)	—	×	×	×	—	terrestrial (woodlands)
Simatherium demissum (buffalo)	—	×	×	×	—	terrestrial (? grasslands)
Kobus subdolus (kob-like)	—	—	×	×	—	terrestrial (woodlands
Kobus sp. B (kob-like)	—	—	—	×	—	near fresh water)
Damalacra neanica (hartebeest-like)	—	—	×	×	—	terrestrial (grasslands)
Damalacra acalla (hartebeest-like)	—	×	×	×	—	
Raphicerus paralius (steenbok)	—	×	×	×	—	terrestrial
Gazella sp. (gazelle)	—	×	×	×	—	(? grasslands)
Ovibovini gen. and at least 2 spp not det.	—	×	×	×	—	terrestrial
ORDER LAGOMORPHA						
Family **Leporidae** (hares, rabbits)						
Pronalagus sp.	—	×	×	×	—	terrestrial
ORDER RODENTIA						
Family **Bathyergidae** (rodent moles)						
Bathyergus sp.	—	×	×	×	—	fossorial
Cryptomys sp.	—	×	—	?	--	
Family **Hystricidae** (porcupines)						
Gen. and sp. not det. A	—	×	—	—	—	terrestrial
Gen. and sp. not det. B	—	—	×	×	—	

	GM	QSM	PPM 3aS	PPM 3aN	PPM undiff.	Inferred habitat preference
Family Cricetidae (rats, mice, gerbils etc.)						
Mystromys sp. A	—	×	—	—	—	⎫
Mystromys cf. *darti*	—	×	—	—	—	⎬ terrestrial
Mystromys cf. *hausleitneri*	—	×	—	—	—	⎬
Gerbillus or *Desmodillus* sp.	—	×	—	—	—	⎭
Dendromus sp.	—	×	—	—	—	terrestrial (? woodlands)
Steatomys or *Malacothrix* sp.	—	×	—	—	—	⎫
Family Muridae (rats, mice)						
Aethomys spp A, B	—	×	—	—	—	⎬ terrestrial
Mus spp A, B	—	×	—	—	—	⎬
Rhabdomys sp.	—	×	—	—	—	⎭
****Euryotomys pelomyoides*	—	×	—	—	—	terrestrial (? near fresh water)
Family Muscardinidae (dormice)						
Graphiurus sp.	—	×	—	—	—	terrestrial (? woodlands)
RODENTIA not det.	—	×	×	×	—	
ORDER CETACEA (whales, dolphins)						
Gen. and spp not det.	×	×	×	×	—	marine

* sp. nov.   ** gen. et sp. nov.

References:
Foraminifera—Tankard 1975*b*.
Other invertebrates—Kensley 1972, 1977; Tankard 1975*b*; unpublished.
Chondrichthyes—Hulley, in Hendey 1976*a*.
Osteichthyes—unpublished.
Amphibia/Reptilia—unpublished.
Aves (Spheniscidae)—Simpson 1971, 1975, 1979.
Aves (other)—Rich 1980; unpublished.
Mammalia (Insectivora, Chiroptera, Lagomorpha, Rodentia—excluding Hystricidae)—Pocock 1976.
Mammalia (Rodentia—Hystricidae)—unpublished.
Mammalia (Primates, Pholidota, Tubulidentata, Hyracoidea, Hippopotamidae, Cetacea)—unpublished, but some details in Hendey 1976*a*.
Mammalia (Carnivora)—Hendey 1972*a*, 1974*a*, 1974*b*, 1977, 1978*c*, 1978*d*, 1980; Hendey & Repenning 1972; Wolff *et al*. 1973; De Muizon & Hendey 1980.
Mammalia (Proboscidea)—Maglio & Hendey 1970; Maglio 1973; Coppens *et al*. 1978.
Mammalia (Perissodactyla)—Hooijer 1972, 1976, 1978; Churcher & Richardson 1978; Hendey 1978*a*.
Mammalia (Tayassuidae)—Hendey 1976*b*; Cooke & Wilkinson 1978.
Mammalia (Suidae)—unpublished, but referred to by Cooke & Wilkinson 1978, and Harris & White 1979.
Mammalia (Giraffidae)—Harris 1976; Churcher 1978; unpublished.
Mammalia (Bovidae)—Gentry 1974, 1978, 1980.

The observations that follow supplement the last summary statement on the composition of the 'E' Quarry fauna (Hendey 1976*a*: 231–243).

Most of the identified invertebrates are conspecific with, or closely related to, living forms and most have counterparts still living in the Langebaanweg area or adjacent ocean. Two new species have been recorded amongst the Mollusca. Marine forms predominate, but estuarine, freshwater and terrestrial

species are also recorded. Palaeoenvironmentally significant species will be discussed later (see p. 68).

Lower vertebrates (fish, amphibians and reptiles) are largely unstudied, although the cartilaginous fish (sharks, skates and rays) and the terrestrial tortoise (*Chersina* sp.) have received some expert attention. Other groups may well be more diverse than the preceding list indicates but, although available material is abundant, it is for the most part fragmentary and identification of taxa may be difficult. With the exception of some sharks (see p. 68), the lower vertebrates apparently represent forms which still occur in the region, or in the adjacent ocean.

The remains of birds are also abundant, a preliminary study having revealed that 'E' Quarry is the richest pre-Pleistocene fossil bird locality in the world (Rich 1980). Although bird remains are less common than those of mammals, and although fewer taxa are presently recognized, they may ultimately prove to be the most diverse group represented in the 'E' Quarry deposits. So far only the penguins have been studied in detail (Simpson 1971, 1975, 1979), and the fact that both identified taxa represent new genera suggests that other birds may be equally distinctive.

The birds are a potentially valuable source of palaeo-environmental information. For example, at least two species of parrots are represented, and parrots no longer occur in the south-western Cape, being confined to wooded tropical and sub-tropical regions further north. While this may indicate a warm, wooded environment at Langebaanweg during the early Pliocene, the representation of marine birds, particularly the Procellariiformes, apparently indicates temperate conditions in QSM and PPM times, which is in keeping with other evidence (see p. 68).

However, a detailed analysis of available material is required before the palaeoenvironmental implications of the avifauna can be assessed. Better identification of the taxa represented is also necessary. For example, there are several passerines that are characteristic of the south-western Cape fynbos region today (McLachlan & Liversidge 1978), and the identification of such forms in the 'E' Quarry avifauna would support the evidence which indicates that the fynbos was being established locally during the early Pliocene (see p. 43).

A curious feature of the avifauna is the under-representation of obvious scavengers such as vultures and crows. Scavengers (hyaenas) are well represented amongst the mammalian carnivores, and the inferred presence of abundant animal carcasses at the time that the deposits were laid down suggests that avian scavengers should also have been common.

The potential importance of the birds as indicators of depositional environments was briefly discussed by Rich (1980).

Mammals are the best represented group in the 'E' Quarry fauna, both in terms of the number of specimens and the number of species. Marine, freshwater, aerial and terrestrial species are recorded, the latter predominating. The

mammals are also the most intensively studied group, although descriptive accounts of about half the identified taxa have yet to be published. There are apparently no extant species represented, and the described forms include four new genera and sixteen new species.

A preliminary study of the small mammals (insectivores, bats, rodents and hares) by Pocock (1976) revealed nothing obviously inconsistent with a late Cenozoic fauna from this region. The most commonly represented of the small mammals are fossorial forms (Chrysochloridae, Bathyergidae), which are today still common in the vicinity of Langebaanweg, and elsewhere in the south-western Cape. The small mammals are a potentially valuable source of palaeoenvironmental information. For example, the only described rodent, a new genus and species (*Euryotomys pelomyoides*) which is common in the QSM, is a primitive otomyinine, a group which is characteristic of well-watered environments. The presence of *Dendromus* and *Graphiurus* may be further evidence for a wooded environment in the area at the time that the deposits were laid down.

One primate only has been recorded from deposits in 'E' Quarry, and it is known from fewer specimens than all other species. The under-representation of this important order is discussed later (see p. 87).

The carnivores are still the most diverse of the mammalian orders repre-sented in 'E' Quarry. They are known from a large number of often complete and well-preserved specimens, a situation which is remarkable in view of the generally poor representation of this group at other African localities of late Miocene and Pliocene age. Since the last summary statement on them (Hendey 1976*a*: 234–240), further studies have been published on the bear (Hendey 1977, 1980), hyaenas (Hendey 1978*c*), mustelids (Hendey 1978*d*), and the seal (De Muizon & Hendey 1980). However, only the accounts of the bear and mustelids can be regarded as complete at this stage. Much material belonging to other families is undescribed, and at least some of the recorded taxa require reinterpretation.

For example, an incomplete study of the civet material has suggested that two species may be represented, one being related to the living African civet (*Civettictis civetta*), while the other may be related to the late Pliocene/early Pleistocene *Pseudocivetta* (Fig. 17). Similarly, the material referred to the canid (*Vulpes* sp.) may also represent two species, one being a generalized form possibly related to later African *Vulpes*, while the second may be related to the late Pliocene/early Pleistocene '*Canis*' *brevirostris*. The difficulty in identifying the 'E' Quarry civet and canid specimens is evidently due to the material representing early stages of lineages which were only clearly differentiated later. This applies in the cases of other 'E' Quarry mammals as well (see p. 82).

Although the identification of, and comments on, the 'E' Quarry probo-scideans made by Coppens *et al.* (1978) are probably substantially correct, this group requires further study. None of the *Anancus* specimens, which apparently represent a new species, has been described, and the relationship

between the 'E' and Baard's Quarry species (Hendey 1978a) has yet to be substantiated. An appreciable number of unstudied teeth of the elephant (*Mammuthus subplanifrons*) are now available, and they may contribute towards resolving the problems surrounding this unsatisfactory taxon.

The 'E' Quarry perissodactyls are palaeoenvironmentally significant since both the rhinoceros and the *Hipparion* are hyposodont forms, indicating the presence of grasslands, whereas most of the other large herbivores are woodland browsers. Although the study of the perissodactyls is largely complete, the *Hipparion* specimens warrant further attention directed at their implications in respect of the succession of strata in the vicinity of Langebaanweg. For example, it is the *Hipparion* from the Anyskop terrestrial deposits which suggests that they are broadly contemporaneous with deposits in Baard's Quarry (see p. 38). In addition, it is the *Hipparion* from the GM which supports the suggestion that this horizon may predate the QSM and PPM by an appreciable period (see p. 23).

The artiodactyls, which are predominantly browsers, are a well-represented and diverse group, ranging in size from a very small peccary to the giant *Sivatherium*. With the exception of the pigs, hippopotamus, and palaeo-tragine, all have now been described, although additional material of most species is available. The palaeotragine is of particular interest since, although Africa is the home of the only living palaeotragine (*Okapia johnstoni*), the post-Miocene history of this group is poorly known, and the 'E' Quarry species is comparatively well represented by both cranial and postcranial material.

Other 'E' Quarry mammals which are unstudied are a pangolin, an aardvark, two species of porcupine, and several cetaceans.

Taphonomy

Taphonomy 'involves all aspects of the transference of organic remains from the biosphere to the lithosphere, and includes both the biological and physical factors and processes that are involved' (Olson 1962: 134). It is, therefore, a branch of palaeontology that is particularly relevant to palaeo-ecological studies. Some information of a taphonomic nature, such as the mode of accumulation of many of the 'E' Quarry fossils, has been given above, and the summary account which follows deals with other matters.

A taphonomic study of the 'E' Quarry fossils such as the now classic one on a late Tertiary vertebrate fauna from Nebraska by Voorhies (1969) has not been undertaken. Nevertheless, almost unavoidably observations of a tapho-nomic nature have been made in the course of fieldwork at Langebaanweg, and subsequently also in the laboratory. Some of these observations have already been recorded elsewhere (Hendey 1974a: 348–353; 1976a: 222–230; 1980: 53–67).

In any assessment of the taphonomy of individual fossil assemblages from 'E' Quarry, it is important that allowance be made for collecting biases, recent damage to bones and the post-depositional disassociation of body parts. Conse-

quently, the manner in which material was acquired needs to be known. specimens were recovered from the 'E' Quarry sediments in the following ways:

1. Surface collecting.
2. Controlled excavation.
3. Uncontrolled excavation.
4. Screening of small sediment samples in the field or the laboratory using mesh of 2 mm or less.
5. Screening of bulk sediment samples in the field using a double-bank of sieves with mesh of 10 and 5 mm.

In the case of surface collecting, material had mostly been exposed by the mining operations, in which case specimens were often out of context, damaged and disassociated from other skeletal elements of the individual involved. A large quantity of material was acquired in this way, with most specimens being of medium to large size. Alternatively, specimens were exposed by wind or water erosion, in which case their condition was often as in burial, and associations of specimens were sometimes preserved. Once again much material was collected in this way, and all except microscopic specimens were recovered.

Only a few controlled excavations were undertaken in 'E' Quarry, two in 1966 and one or two in the years 1969, 1970, 1975, and 1976. However, although most of the fossiliferous horizons and areas of the QSM and PPM were sampled, the size of the excavations was very variable, ranging from a few to hundreds of cubic metres of deposit. The condition of specimens for the most part reflects that in burial, and associations were recorded. Uncontrolled excavations differed in that they were always on a small scale, usually being centred on a significant fossil discovered on the surface (Fig. 13). Except for the recording methods, they could be considered as controlled excavation when carried out by qualified personnel, but otherwise they served only to build up sample sizes.

It was the latter factor, together with the need to recover small fossils, that was the motivation in the screening of sediment samples. The screening of small samples usually involved the use of hand-sieves washed in ponds on site, or in containers of water in the laboratory. Since the deposits were mostly unconsolidated fine- to medium-grade sands, little agitation of the sieves was required and damage to specimens was minimal. However, associations of body parts were usually lost.

The co-operation of the mining company made the screening of bulk sediment samples possible. This was done when mining or other factors threatened fossiliferous deposit, and involved the removal by mechanical means of samples ranging in size from a few tons to hundreds of tons, and the transportation of the sample by truck to an area where a stand with double-banked two-man sieves was set up. Piped water was used to wash the 'dumps' through the sieves. This process allowed the recovery of some very large samples of fossils, and was particularly useful in the recovery of rare taxa. However, the process which variously involved mechanical excavators, bull-

Fig. 13. The skull and vertebral column of a buffalo *Simatherium demissum*, (SAM–PQ–L23400) *in situ* in the QSM.

dozers, front-end loaders, and tip-trucks, was very destructive. In addition, there were instances where the removal process was not carefully controlled and fossiliferous sediments of the QSM and bed 3aN were mixed.

The provenance of material was one of the recurrent problems encountered in the fossil-collecting programme. Material of doubtful provenance includes much of that collected prior to 1969, but the problem continued even when the nature of the succession was well known and exact sites of discovery were recorded. Both beds 3aS and 3aN truncated the QSM, while bed 3aN truncated bed 3aS, and it was in such situations that doubts about provenance arose. Nevertheless, assemblages of known provenance do exist, and it is these that will ultimately be used in the detailed analyses of fossils from particular horizons. A problem which may be impossible to deal with is that of material reworked from pre-existing deposits. It affects mainly bed 3aS, which includes specimens derived from the QSM.

The depositional environments of the 'E' Quarry succession need not be discussed again, but some comments on the agencies responsible for concentrating fossils in certain areas are necessary.

The principal agency involved was water action. In the case of the GM fossils, concentration was by wave action, and in QSM III it was the combined effects of the river and tides which led to the accumulation of fossils. Elsewhere in the QSM and in beds 3aS and 3aN the river was largely responsible for concentrating fossils deposited in a subaqueous environment, although a subsidiary role for wave and tidal action cannot be ruled out.

One of the common field practices in taphonomic studies is the recording of the orientation of *in situ* fossils, since the resultant data may indicate whether or not the fossils were deposited by flowing water, and, if so, the current direction(s). In one of the earlier controlled excavations in 'E' Quarry (LBW/E/1969/1) some such recording was done, but the procedure was abandoned since it was found to be time-consuming and probably pointless. It seemed obvious at that time that the deposits in question (bed 3aS) were channel-laid and that the trend of the channel was north-east to south-west. All subsequent observations on the bed 3aS deposits confirmed this early impression. Much the same applied in the case of the bed 3aN deposits (see Hendey 1976*a*: 228–230; 1980: 57–63), although in this instance the nature and distribution of the fossils were much more obviously indicative of a fluviatile environment.

Evidence for the subaerial accumulation of some QSM fossils has been discussed elsewhere (Hendey 1974*a*: 349–353; 1976*a*: 223–224). This includes the record of a vertebrate microfaunal concentration, apparently an owl pellet accumulation, which was burnt prior to incorporation in the deposits. Microfaunal concentrations of this kind were not common in 'E' Quarry. The most notable examples were two that occurred at the interface between the QSM and bed 3aS. These assemblages, designated 1/1968 and 12/1968, were discussed by Hendey (1970*a*: 81, 86–88), and remain something of a mystery. They are probably comprised largely of the residues of owl pellet accumulations which were transported a short distance and redeposited by minor drainage channels in QSM or bed 3aS times. This process would account for the admixture of larger fossils which obviously did not feature in the diet of owls. Two species of owls are recorded from the QSM.

Otherwise there is no evidence for animals having been 'bone collectors' during the period of deposition of the 'E' Quarry deposits. Elsewhere in the south-western Cape concentrations of fossils in porcupine lairs and hyaena dens have been recorded (Hendey 1974*a*; Klein 1975). Some of these are in rock shelters, of which none existed in the 'E' Quarry area, while others are found in what are presumed to be aardvark burrows. Such burrows would not be expected in the largely subaqueously deposited PPM, and it is unlikely that any existed on the floodplain of the river in QSM times. An aardvark is recorded from the QSM, but it is an extremely rare element in the fauna. The aardvark remains from beds 3aS and 3aN were probably washed into the area by the river.

Large numbers of fossils were found in certain exposures of the QSM, although not necessarily concentrated in restricted areas. For example, the remains of small mammals and birds were abundant in the QSM I collecting area named 'East Stream' (Hendey 1974*a*, fig. 3). The East Stream fossils probably represent a microenvironment (floodplain grassland or thicket) in which predation by small carnivores (mainly mongooses) occurred frequently. Larger mammals that died there include an elephant (*Mammuthus subplanifrons*) several pigs (*Nyanzachoerus* cf. *pattersoni*), a large cat (*Dinofelis dias-*

temata), and hyaenas (*Hyaena abronia*). Some redistribution of animal remains apparently took place when this area was inundated during floods (Hendey 1974*a*: 351–352; 1976*a*: 223–225).

An impression gained during field and laboratory work was that the body part representation of vertebrates varied according to the source of material. The only body part analyses undertaken to date are those of bird remains from the QSM I and QSM II assemblages (Rich 1980), to which may be added the detailed record of the number and condition of penguin bones from QSM I given below. Many more such analyses are required before meaningful tapho-nomic interpretations are obtained, but some general statements on body part representation are already possible.

Complete skeletons were not found, although partial skeletons were recovered from both the QSM and PPM. The most complete was that of the holotype of *Hyaena abronia* from QSM I, which comprises the skull and about eighty postcranial bones (Hendey 1974*a*: 103–115, 351–352). Otherwise elements of individual skeletons tended to be completely disassociated, or represented by only a few bones such as parts of a vertebral column or limb. Even in the latter instances it was exceptional to find bones still articulated. An example of a partial skeleton from the QSM in which some elements were in articulation is that of the buffalo illustrated in Figure 13. It is one of several medium to large mammals from the QSM which probably represent the remains of animals killed *in situ* and subsequently dismembered by the primary predator and by scavengers (Hendey 1974*a*: 351).

By contrast, the recently described partial skeleton of an *Agriotherium* (SAM–PQ–L45062) from bed 3aN, in which all remaining skeletal elements were disassociated (Hendey 1980: 62–63), was a more common type of occur-rence. In this instance, the specimen was transported to its point of deposition by the river and it might well have been complete when deposited, but suffered subsequently from a variety of destructive post-depositional processes, includ-ing disarticulation after loss of soft tissue, fire, pressure of overlying deposits, and, more recently, the mining operation and collecting.

It is virtually certain that the skull of L45062 was intact at the time of deposition and that its subsequent fragmentation was due largely to the pressure of overlying deposits. Complete, or nearly complete, skulls are not common in the 'E' Quarry assemblage, and all the known specimens suffered some degree of crushing. Restoration of these specimens was, however, facilitated by the fact that fragments were easily recovered from their unconsolidated matrix and were usually undistorted. Missing parts were probably lost during the recovery process rather than earlier. One of the most complete skulls recovered is illustrated in Figure 17, while others have been illustrated elsewhere (e.g. Hendey 1974*a*, figs 19–20; Gentry 1980, figs 28–29; De Muizon & Hendy 1980, figs 1–3, 5). One instance is known where an exceptionally robust skull might have been intact in the deposits but was damaged by the mining operation. This is the skull of the *Plesiogulo*, SAM–PQ–L40042, described by Hendey (1978*d*: 330–336).

In general, the fossils from 'E' Quarry are well preserved, although damage caused by post-mortem processes is not uncommon. These processes include the mining operation and collecting methods which led to the recovery of specimens, and they are obviously of no taphonomic significance. Nevertheless, it is important that they be recognized and not be confused with that post-mortem damage which is relevant to taphonomic studies.

This damage is significant since it reveals some of the physical, chemical and biological processes which affected animal remains from the time of death until their discovery. From a palaeoecological point of view it is the factors operating at the time of death and shortly thereafter that are important, since they may reveal something of prevailing biological interactions and physical conditions. For example, the activities of predators and scavengers may be revealed by distinctive types of damage and thus provide evidence of trophic relationships, while the condition of specimens may also indicate the nature of depositional environments, which are a reflection of the prevailing physical environment.

The bed 3aN *Agriotherium* may again be cited as an example, since the recently discussed post-mortem damage to the specimens (Hendey 1980: 63–66) is typical of that encountered amongst the larger mammals from 'E' Quarry. Similar and additional types of damage were discussed elsewhere (Hendey 1974*a*: 349–353). Table 4 lists various types of post-mortem damage evident in specimens from 'E' Quarry. Only one of the more unusual types of damage is discussed below, since the example cited has not previously been recorded.

Hendey (1974*a*: 353) mentioned a series of bones from the QSM which had apparently been etched by the stomach acids of a hyaena. Such specimens are not common, but one striking example involves the penguins from 'E' Quarry. Two penguin species are recorded, namely, *Inguza predemersus* and *Dege hendeyi* (Simpson 1971, 1975, 1979), and a high proportion of the bones in the available assemblages have been etched, evidently by stomach acids (Fig. 14). By contrast, this type of damage is either rare or not recorded in bones of other birds from the same deposits.

The most likely explanation of this difference in condition is that the penguins were preyed upon by an animal that ingested their carcasses and later regurgitated the indigestible remnants, whereas other bird bones found in the deposits were not ingested by predators. It is only the stouter and more durable bones of the penguin skeleton which have been recorded (i.e. mainly limb bones). While other bones of the skeleton are less diagnostic, and therefore less likely to be recognized as belonging to penguins, their absence is probably due to their having been destroyed by the stomach acids which damaged most of the surviving bones. The most delicate of bones belonging to other birds are preserved together with those of penguins, which indicates that the effects of depositional processes can be eliminated as the cause of the condition and representation of penguin bones.

Modern penguins are preyed upon by sharks and other large predaceous fish, and seals (Simpson 1976), and these animals are all possible predators in

TABLE 4

Examples of post-mortem damage exhibited by fossils from 'E' Quarry, Langebaanweg.

TYPES OF DAMAGE	Cracked and exfoliated bones and teeth	Crushed bones	Abraded bones and teeth	Bones and teeth discoloured black* and/or grey, and often cracked and exfoliated	Etched bones
PROBABLE CAUSES AND ILLUSTRATIONS	Pre-depositional subaerial weathering; post-depositional subaiqueous weathering (e.g. in lag deposits)	Post-depositional pressure of overlying deposits (especially affecting mammal skulls—e.g. Hendey 1980, fig. 2)	Wave action; river transport; sand-charged water flowing over specimen after deposition (Hendey 1970a; fig. 3)	Fire (Hendey 1980; fig. 30)	Stomach acids of carnivores (Fig. 14) (Simpson 1975; figs 4-5; 1979, fig. 1)
TYPES OF DAMAGE	Spirally fractured long bones	Punctate marks on bones	Irregular grooves, randomly orientated on bones, sometimes with irregular loss of adjacent bone	More or less parallel grooves on bones	Regular grooves, randomly orientated on bovid horn-cores
PROBABLE CAUSES AND ILLUSTRATIONS	Biting by carnivores (Hendey 1974a, fig. 77A)	Biting by carnivores (Hendey 1974a, fig. 77B)	Biting and gnawing by carnivores (Hendey 1974a, figs 77C, D; 1980, fig. 28)	Gnawing by rodents (Hendey 1980, fig. 29)	Keratophagous insect larvae (Fig. 12)

*Fossils from the 'peat beds' of the QSM and PPM, bed 3aN are also black, but they are usually readily distinguishable from burnt specimens.

Fig. 14. Undamaged (above) and acid-etched (below) penguin tibiotarsi, femora and carpometacarpi from the QSM (East Stream sample).

the case of the 'E' Quarry penguins. In addition, penguins are preyed upon by terrestrial animals, and 'E' Quarry is unique amongst recorded Tertiary penguin localities in that the penguin bones come from non-marine deposits (Simpson 1976) occurring in association with a wide variety of terrestrial vertebrates, including predaceous forms. Consequently, it could also be significant that 'E' Quarry is apparently the only known locality from which penguin bones etched by stomach acids have been recorded. In fact, the 'E' Quarry penguins are likely to have been preyed upon by several aquatic and terrestrial predators, although only one is likely to have caused the acid-etched bones. This was probably an animal that bolted its food, and subsequently regurgitated indigestible residues. This behaviour applies in the case of sharks (P. A. Hulley, pers. comm.), and of the predators recorded in association with the 'E' Quarry penguins, sharks are here favoured for the role.

Further clues concerning predation on the 'E' Quarry penguins may emerge from more detailed examinations of the available material and comparisons with stomach contents of modern penguin predators. Even the most superficial examination of the 'E' Quarry penguin assemblages reveals features that may be of taphonomic significance. For example, etching is more pronounced on leg bones than those of the flipper (Table 5). In addition, certain

TABLE 5

Limb bones of adult penguins (QSM I, East Stream sample) from 'E' Quarry, Langebaanweg.

	Inguza predemersus			*Dege hendeyi*		
	Specimens with little or no etching	Specimens with pronounced etching	% etched	Specimens with little or no etching	Specimens with pronounced etching	% etched
Humerus . .	3	6	67	—	—	—
Ulna . . .	6	10	63	—	1	100
Radius . .	6	8	57	1	—	0
Carpometacarpus	4	3	43	—	—	—
Total flipper .	19	27	59	1	1	50
Femur . .	3	9	75	3	7	70
Tibiotarsus . .	2	19	90	1	4	80
Tarsometatarsus .	1	15	94	2	4	67
Total leg . .	6	43	88	6	15	71

TABLE 6

Etching on penguin leg bones (QSM I—East Stream sample) from 'E' Quarry, Langebaanweg.

	Inguza predemersus			*Dege hendeyi*		
	Little or no etching	Pronounced etching	% etched	Little or no etching	Pronounced etching	% etched
Femur, proximal end .	4	5	56	7	1	14
Femur, distal end . .	2	7	78	2	6	75
Tibiotarsus, proximal end .	1	9	90	1	1	50
Tibiotarsus, distal end . .	4	8	67	1	3	75
Tarsometatarsus, proximal end .	—	13	100	—	5	100
Tarsometatarsus, distal end . .	5	10	67	1	5	83

parts of individual bones are more affected than others. For example, the proximal ends of femora are less often etched than distal ends, while all the proximal ends of the tarsometatarsi are etched, and, at least in the case of *Inguza predemersus*, the proximal ends of the tibiotarsi are more affected than distal ends (Table 6). Furthermore, although there is a general similarity in the condition of the bones of the two penguin species, there are very marked differences in the representation of individual bones. This may simply be due to the smaller *Dege hendeyi* sample size, but it is striking that whereas there are nearly as many femora of *D. hendeyi* (ten) as there are of *I. predemersus* (twelve), other limb bones of the former are appreciably less common. This applies particularly in the case of flipper bones (Table 7).

TABLE 7

Flipper and leg bones of penguins (QSM I—East Stream sample) from 'E' Quarry, Langebaanweg.

	Inguza predemersus	*Dege hendeyi*	*Dege: Inguza*
Total flipper . .	46	2	1:23
Total leg . . .	95	21	*c.* 1:5
Flipper: leg . .	*c.* 1:2	*c.* 1:10	

The above observations are not interpreted here, but they presumably reflect events which followed shortly after the deaths of the birds concerned, and thus indicate a potential value in analyses of this kind.

Certain of the 'E' Quarry fossils also reveal something about the condition of animals during their lifetimes, and although this does not necessarily fall within the scope of taphonomy, it is convenient to mention it here. The majority of specimens show no signs of abnormality, but pathological conditions amongst carnivore specimens have already been recorded (Hendey 1974*a*: 184–185; 1978*d*: 336; 1980: 53), while abnormalities observed amongst herbivores will be mentioned later (see p. 76). The latter are ascribed to dietary factors, but most of the other recorded conditions are evidently due to old age or injury. Apart from their intrinsic interest in the field of palaeopathology, dental and osteological abnormalities are significant since they may provide evidence of prevailing environmental conditions, the age structure of populations, cause of death, and behaviour patterns. Consequently, a detailed study of relevant specimens is clearly desirable.

PALAEOENVIRONMENT

The nature of environments in the south-western Cape and adjacent regions during the Palaeozoic, Mesozoic, and early Cenozoic are known only in a very general way, but the record for the late Cenozoic is better (Deacon 1979). However, even for this period the record is only intermittently detailed,

and for the late Tertiary it is the deposits in the vicinity of Langebaanweg that provide the most substantial body of information.

The environment at Langebaanweg at the time that the Varswater Formation and other late Tertiary deposits were laid down was clearly very different from that of the present. An account of the physical setting of the area and of the geological history of these deposits was given earlier, and the present section will deal with the climate and the environmental implications of the Varswater Formation flora and fauna. It is important to note that information presented below contributed to the revised interpretation of the geological history of the Langebaanweg area. In other words, although these two aspects of the present study are interrelated, the interpretation of the geological history stemmed in part from the palaeoenvironmental study rather than the reverse, which is implied by their order of appearance in this report.

The late Miocene and early Pliocene (i.e. between about 10 and 4 Ma) was a period of great change over much of the earth's surface. It was the time when the generally moderate climatic conditions which characterized most of the Tertiary were coming to an end, and when the most recent of the world's 'ice ages' was beginning. This 'ice age' has been a period of marked oscillations in world climates, and these have had a profound effect on the biology of the earth.

The Miocene–Pliocene boundary is defined on the basis of the marine sedimentary succession in the Mediterranean Basin, and it is now generally taken to date back about 5 Ma, with marine microfossils and palaeomagnetic data having facilitated widespread correlations (e.g. Berggren & Van Couvering 1974). Apart from changes in marine microfaunas, the terminal Miocene was characterized by a world-wide marine regression, a phenomenon that was caused by increased glaciation in Antarctica (see below), and which had significant effects in coastal and continental shelf regions of the world.

In the Mediterranean this regression contributed to the so-called 'Messinian [or Mediterranean] salinity crisis', which 'was an interval of highly restricted circulation reflected in extensive deposition of stagnant water and evaporative sediments' (Van Couvering et al. 1976: 263). This event, which lasted approximately 1,5 m.y., was concluded by 'a return to former water depths coincidentally with the beginning of the Pliocene . . . which is calibrated to t = 5 Ma' (Van Couvering et al. 1976: 263). Hsü et al. (1977: 402) have stated that the Messinian salinity crisis is 'such a geologically recent catastrophic event [that it] had a great impact on the modern world, . . . on regional and global climates and on the evolution and distribution of plants and animals'.

An example of the biological impact of this event was that it allowed the late Miocene faunal interchange between Africa and Eurasia which will be mentioned later (see p. 84), and hence the presence in the 'E' Quarry fauna of certain 'Eurasian' taxa. However, the principal significance of the Messinian event here is that it is well documented and thus illustrates the nature and timing of certain of the *global* phenomena that occurred during the late

Miocene and early Pliocene. For example, the Messinian event was simply one result of the increased late Miocene Antarctic glaciation and the consequent global marine regression, which are events of far greater significance in the present instance. Langebaanweg is situated in southern mid-latitudes, 7 500 km south of the Mediterranean, whereas it is only 4 000 km from Antarctica, and separated from it by an ocean that influences the climates of both regions. In addition, its near-coastal location makes it subject to the effects of sea-level changes.

In a recent review of late Cenozoic palaeoenvironments on the west coast of southern Africa, Tankard & Rogers (1978) related the aridity of this region to the history of the Southern Ocean and the Antarctic ice-cap. Although there are many conflicting statements on the timing of Antarctic ice-cap origin and growth (see Mercer 1978), there is evidence that maximum growth was achieved late in the Miocene (see McLachlan & McMillan 1979, fig. 2). Once the Antarctic ice-cap had formed it 'remained a semi-permanent feature exhibiting some changes of volume', 'the most important [being] during the latest Miocene (t = 5 MY ago) when ice volumes increased beyond those of the present day' (Kennett 1978: 41). This was followed by 'a regressive ice phase with extensive melting and iceberg calving' (Hayes et al. 1973: 24). The glacial maximum led to the terminal Miocene global marine regression (cycles TM3.2, TM3.3 of Vail & Hardenbol 1979), while the subsequent regressive ice phase caused the early Pliocene global transgression (cycle TP1).

The fact that these events are correlated not only with the Messinian salinity crisis and its conclusion, but also with coastal strata elsewhere (e.g. New Zealand—see Loutit & Kennett 1979), suggested that correlation with Miocene–Pliocene strata in South Africa is also feasible.

Relevant here is evidence that local sea temperatures declined during the period of deposition of the Varswater Formation.

Present sea temperatures on the Cape west coast are low, and the area falls within the Cold Temperate Province of the southern African coast (Brown & Jarman 1978). However, the coast near Langebaanweg is close to the southern boundary of this province and the western limit of the 'overlap region' between the Cold and Warm Temperate Provinces (Brown & Jarman 1978: 1246). This 'overlap region' includes areas where the proportion of cold west coast species is high, and others, such as False Bay, where 'south coast species are much in evidence' (Brown & Jarman 1978: 1261). The northern shore of False Bay is at present only about 130 km south of Langebaanweg, and during the past when sea-levels were substantially higher, this bay was linked across the Cape Flats with Table Bay, 20 km further north. Furthermore, Langebaanweg is today only 13 km inland from the 'almost landlocked body of water comprising Langebaan Lagoon and Saldanha Bay', with its 'biota of great richness, diversity and productivity' that includes species that 'are characteristic of other provinces, notably the south coast warm-temperate region' (Brown & Jarman 1978: 1267).

Langebaanweg is thus situated in an area where the local marine fauna is potentially subject to marked differences in composition depending upon

prevailing climatic and environmental factors. Even today elements of two contrasting faunas (warm and cold temperate) are represented near by (Lange-baan Lagoon, Saldanha Bay), or not far away (False Bay), while the local occurrence of thermally anomalous molluscs during the late Pleistocene has been documented by Tankard (1975*d*).

Molluscs of the GM are mostly of taxa found along the adjacent coast today, but some 'suggest water temperatures considerably warmer (about 3–5 °C) than today. These warm water molluscs include *Cellana capensis*, *Turbo sarmaticus*, *Barbatia obliquata*, *Ostrea atherstoni*, and *Striostrea margaritacea*' (Tankard 1974*a*: 281). The oysters *Ostrea* and *Striostrea* are not known from 'E' Quarry exposures of the GM, but are from equivalent deposits on the near-by farm of Sandheuwel (Tankard 1974*a*). *Cellana capensis* is today found north of Port Alfred on the east coast (i.e. the Subtropical Province), while the other four species occur eastwards from False Bay (i.e. the Warm Temperate and Subtropical Provinces) (Kensley 1973; Day 1974; Brown & Jarman 1978).

In addition, although the sharks of the GM have yet to be studied in detail (Hendey 1976*a*: 233), three of the species that have been recorded are today characteristic of warmer oceanic regions. They are *Carcharhinus melanopterus*, *C. limbatus*, and *Squatina africana* (Bass *et al*. 1973, 1975).

Indications are, therefore, that the GM was laid down during a warm phase (i.e. warm temperate to subtropical), probably the period late in the Miocene that preceded the onset of colder conditions towards the end of this epoch.

Molluscs of the QSM are also mainly of taxa found along the adjacent coast today, although one is a warmer water species. This is *Pyrene albuginosa*, which presently ranges from False Bay to Natal. On the other hand, the QSM assemblage, unlike that of the GM, also includes two essentially cold-water species, namely, *Chiton nigrovirescens* and *Tricolia capensis*, which are largely confined to the Cold Temperate Province of the west coast. In this instance, *T. capensis* is particularly significant, since it is the most commonly occurring of the QSM marine species (Kensley 1977).

It is, therefore, likely that local sea temperatures at the time of deposition of the QSM were somewhat lower than those prevailing earlier when the GM was laid down, and might have been little different from those of the present (i.e. cold temperate). Consequently, the QSM is likely to date from the period when the effects of Antarctic glaciation were being manifested in southern mid-latitudes (i.e. terminal Miocene or later).

A similar, and probably contemporaneous, change from warm to cold water is recorded on the west coast of South America. Mercer (1978: 80). quoting W. J. Zinsmeister, noted that the 'presence of distinctly warm-water genera of molluscs indicates that during Middle and Late Miocene time the coastal waters of southern Chile were warm subtropical', and that these 'warm-water faunas were replaced by distinctly cool temperate faunas in latest Miocene or earliest Pliocene time'.

Although no identifiable molluscs are recorded from deposits overlying the QSM (i.e. the PPM), remains of another marine species, the seal (*Homiphoca capensis*), suggest that either there was a further temperature drop in the period between deposition of beds 3aS and 3aN, or that temperatures remained consistently cold during this period. The evidence for this concerns the greater development of the maxillo-turbinals in the bed 3aN population of *H. capensis* (De Muizon & Hendey 1980: 123). This adaptation to low sea and ambient air temperatures may either reflect a lowering of such temperatures during the period in question, or a delayed reaction to the prevailing cold conditions. In the case of the latter alternative, the implication is that the cold adaptation in *H. capensis* lagged behind the onset of the cold. This may be a more reasonable supposition in the case of a large mammal than the one that would have the adaptation immediately coincident with the temperature change.

It is worth noting in this connection that *H. capensis* was almost certainly resident in the Langebaanweg area, and consequently that the cold adaptation reflects local conditions. *H. capensis* was definitely not represented by occasional vagrant individuals as is the case today with certain Antarctic and sub-Antarctic seals recorded on the Cape coast (e.g. *Mirounga leonina*, *Lobodon carcinophagus* and *Hydrurga leptonyx*). The presence of the remains of very young, probably neonate, individuals in the 'E' Quarry assemblage indicates that breeding took place in the immediate vicinity. Otherwise the individuals represented range from young to very old, and at least in beds 3aS and 3aN they are present in large numbers, indicating large local populations at the time of deposition.

In addition, it is unlikely that *H. capensis* was seasonally migratory. Its dental and postcranial characteristics suggest it was a coastal species, unlike its closest living relatives, the pelagic crabeater and leopard seals (*Lobodon carcinophagus* and *Hydrurga leptonyx*) (De Muizon & Hendey 1980). These two species are migratory, moving southwards during summer when the pack-ice begins to break up (King 1964). Southward migration during summer was probably characteristic of all the southern middle and high latitude migratory seals that are now extinct, and since beds 3aS and 3aN were probably laid down during summer (see p. 73), *H. capensis* evidently did not follow this practice.

Other evidence of prevailing temperatures may yet be obtained from a study of the QSM and PPM avifaunas. There are indications that the avifaunas also reflect cold conditions (see p. 54), but this has yet to be substantiated.

Available evidence therefore indicates a lowering of sea temperatures during the period between deposition of the GM and QSM, and either a further drop between deposition of beds 3aS and 3aN, or consistently low temperatures at that time. Although there is as yet no positive evidence of what occurred between deposition of the QSM and bed 3aS, it is unlikely that there was a deviation from the generally cold conditions otherwise indicated, since the QSM, bed 3aS and bed 3aN represent deposition during a single geological episode (i.e. a marine transgression). Sea temperatures were low at this time

apparently because it followed immediately after the terminal Miocene glacial maximum in Antarctica. Temperatures might have risen again later in the early Pliocene transgression (see p. 16).

Thus, while deposition of the GM probably took place before the onset of the terminal Miocene glacial maximum, the QSM and PPM are likely to post-date this event. This conclusion, taken in conjunction with others discussed in this report, contributed to the correlation of the 'E' Quarry deposits with the late Miocene–early Pliocene events in Antarctica, the Mediterranean Basin and elsewhere. This correlation is summarized in Table 8, which formed the basis of the correlation of the entire late Tertiary succession in the Langebaanweg area with the global sea-level changes recorded by Vail & Hardenbol (1979) (Fig.3, Table 2).

To sum up, the GM is here interpreted as representing an event dating back to a warm phase during the late Miocene, while the post-GM regression is correlated with the world-wide lowering of sea-level which coincided with the glacial maximum in Antarctica during the terminal Miocene (i.e. between 5,5 and 5 Ma—see Van Couvering et al.1976). Amongst other significant events, this regression has been correlated with the climax of the Messinian salinity crisis, and the formation of phosphate nodule beds in Australia and alsewhere in the world (Carter 1978). The transgression during which the QSM and PPM were laid down is in turn correlated with the regressive ice phase in Antarctica during the early Pliocene, between 4,5 and 5 Ma (Van Couvering et al. 1976). This transgression, which is recorded in countries as far apart as Spain and New Zealand (Loutit & Kennett 1979), brought the Messinian salinity crisis to an end. This interpretation of events indicates that the main exposures of the Varswater Formation in 'E' Quarry (i.e. the QSM and PPM) are of the same age as the early Pliocene deposits in the Mediterranean Basin (including those at Montpellier in France), and at least part of the Opoitian Stage in New Zealand. Correlation with other early Pliocene coastal deposits is clearly possible.

One possible inconsistency with this interpretation concerns the suggestion that sea temperatures might have declined during the period of deposition of the QSM and PPM. Since the early Pliocene transgression post-dates the late Miocene glacial maximum in Antarctica, it would be expected that sea temperatures in southern mid-latitudes would be rising at this time. However, according to Hayes et al. (1973: 24) 'the waters around [Antarctica] would not necessarily exhibit warming at that time but simply a slowdown in the rate of cooling'. At issue here is the nature and timing of events in Antarctica during the late Tertiary, and, according to at least some interpretations, Southern Ocean surface temperatures did decline during the early Pliocene (Mercer 1978: 84–86, fig.4). This is consistent with palynological evidence from the south-western Cape that suggested to Coetzee (1978: fig.2) that the local climate changed from 'Cool Wet' during the late Miocene to 'Colder Drier' during the Pliocene.

There is abundant evidence from various parts of the world that the Miocene and Pliocene were epochs when terrestrial environments were under-

TABLE 8

The Varswater Formation, 'E' Quarry, Langebaanweg.

STRATIGRAPHIC UNITS	PRINCIPAL DEPOSITIONAL ENVIRONMENTS	SEA-LEVEL	SEA TEMPERATURES	CLIMATE	POLLEN ZONES** AND VEGETATION	AGE
PELLETAL PHOSPHORITE MEMBER (PPM undifferentiated) / PPM, 3aN / PPM, 3aS	Marine littoral / Fluviatile / Fluviatile / Estuarine and terrestrial	Transgression (cycle TP1*)	Cold temperate	Temperate; colder and drier than before**	Lvii (in part)** Temperate woodlands and grasslands; first strong development of the fynbos**	Early Pliocene (c. 5,0 Ma) Time interval / Time interval
QUARTZOSE SAND MEMBER (QSM)	No deposits	Regression (cycles TM3.2, 3,3*)	Probably cold temperate	Temperate	Temperate woodlands and grasslands	Terminal Miocene (6, 6–5, 2 Ma)
GRAVEL MEMBER (GM)	Beach	Stillstand during regression (cycle TM3.1*)	Warm temperate to subtropical	Warm temperate to subtropical (becoming cooler)	Lvi (in part)** Subtropical monsoon forest and grassland	Late Miocene (9, 8–6, 6 Ma)

VARSWATER FORMATION

*Vail & Hardenbol (1979)

**Coetzee (1978)

going significant change. For example, Webb (1977: 355) has recorded that 'early in the Cenozoic Era North America was covered almost entirely by forest', and that 'during the mid-Cenozoic . . . an increasing proportion of the land opened up, forests giving way to woodland savanna, thorn forest, and thorn scrub', while 'by the late Cenozoic forested areas had decreased still further and much of the savanna was being replaced by grassland steppe and even desert'. Webb (1977: 371) also states that 'the last step in dismantling the once continuous forests of North America came in the Pliocene, about five million years ago'. He goes on to note that 'a remarkably similar series of changes affected the fauna of temperate South America during the same 40-million-year interval' (Webb 1977: 355).

Kemp (1978) has recorded the environmental changes undergone in the south-east Indian Ocean region during this period and, amongst other observations, she noted that the 'latest Miocene was marked by an intense and sudden chilling [which] must have caused marked precipitation decrease in much of Australia' (Kemp 1978: 170). These and subsequent climatic events had a pronounced affect on the vegetation of the continent. For example, Axelrod & Raven (1978: 112) recorded that 'evidence in south-eastern Australia . . . [indicates] that the transition from a humid temperate rainforest to the present dominant *Eucalyptus-Acacia* vegatation occurred at ~ 4.5 m.y. (Gill 1975)'.

There were comparable changes in Europe at this time. Delson (1975: 46) has suggested that the deterioration in the European environment late in the Miocene was determined largely by 'relative decrease in moisture', there being 'a gradient from well-watered deciduous (or even evergreen) woodland in the north, through parkland, scrub and into steppelike vegetation . . . with gallery forests along watercourses'. The situation in southern Europe is relevant in the present instance, since those areas bordering the Mediterranean now have a climate similar to that of the south-western Cape, and changes undergone in the two regions during the late Tertiary are likely to have been comparable.

The faunas of Langebaanweg and Montpellier in southern France are broadly contemporaneous and similar in composition (see p. 89), and these localities are similarly situated in near-coastal environments which today have a Mediterranean type of climate. Consequently, it is possible that conclusions reached concerning the palaeoenvironment of Montpellier early in the Pliocene are relevant in the case of Langebaanweg.

Delson (1975: 47), quoting Lobreau-Callen & Suc (1972), states that pollens from Montpellier indicate a 'monsoon/dry season climate', 'closely analogous to that of . . . North Vietnam'. Schulze & McGee (1978, table 1), following Köppen & Geiger (1936), have monsoon climate characterized by 'mean temperatures above 18 °C for all months', with 'forest-vegetation despite [a] dry season'.

There is evidence to suggest that these conditions might have prevailed in the Langebaanweg area during the period of deposition of the middle to late Miocene elements in the succession (i.e. the GM and the upper levels of the

pre-GM deposits), but that by the early Pliocene (i.e. QSM, PPM) they were changing, with the present climate and vegetation patterns being in the process of development.

The predominance of browsers amongst the QSM and PPM herbivores indicates that forests or woodlands existed in the area during the early Pliocene, probably having been present locally for an appreciable period. This is confirmed by palynological evidence from the upper levels of the pre-GM deposits, which also indicates that the forests of the time included tropical elements such as palms (J.A. Coetzee, pers. comm.). The local vegetation during at least a part of the middle to late Miocene might therefore have been of a monsoon-forest type. The presence of grazers in the QSM and PPM faunas indicates that by the early Pliocene grasslands had developed locally, while there is palynological evidence for fynbos vegetation types making an appearance (see p. 43).

At the time of deposition of the QSM and PPM, rainfall was strongly seasonal, with the wet season probably being summer. However, the rainfall regime was then apparently changing, and the summer-wet/winter-dry pattern was probably more characteristic of the late Miocene than the early Pliocene. This possiblity, together with the likely vegetation, suggests the monsoonal combination of forest/dry season quoted above.

It has yet to be certainly established when the summer-dry/winter-wet rainfall pattern was first established in the south-western Cape, but there can be little doubt that the QSM and PPM date from a period when the transition was taking place; or was about to take place. According to Taylor (1978: 75) 'dry summers are of recent origin in southern Africa and probably only appeared at the beginning of the Pleistocene'. Axelrod & Raven (1978: 112) are more cautious in stating the 'there is no evidence that the summer-dry (mediterranean) climates in southern Africa existed before the formation of a major ice sheet on Antarctica (~ 5 m.y.)'. Although the fynbos vegetation is today centred on the south-western Cape winter-rainfall region, it evidently had its origins under summer-rainfall conditions (Levyns 1964; Axelrod & Raven 1978; Taylor 1978). Consequently, the fact that fynbos was being established in QSM times does not necessarily mean that the summer-dry/winter-wet pattern already existed then.

The situation in respect of prevailing temperatures during the Miocene and early Pliocene is less complex. It was suggested earlier that temperate conditions prevailed in QSM and PPM times, and conditions then may have been little different from those of today. The present mean annual temperature in the south-western Cape is about 17 °C, with a mean annual range of about 8 °C near the coast (Fuggle & Ashton 1979). The region is thus cooler than those with monsoon climates, but the temperature difference is not great. During warmer phases such as that during the Miocene when the GM and upper levels of the pre-GM deposits were laid down, temperatures characteristic of monsoon climates might well have prevailed.

Langebaanweg during the Miocene, like Montpellier during the early Pliocene, might therefore have had a monsoon climate and vegetation. The essential difference between these two localities was in the timing of a drop in temperature and its consequent affect on rainfall and vegetation. The glaciation of the Arctic lagged behind the glaciation of Antarctica, with the expansion of the Arctic ice-cap and sea-level ice dated to 3 Ma (Berggren & Van Couvering 1974). Thus, while conditions at Montpellier during the early Pliocene were still 'tropical', at Langebaanweg they had already moderated to 'temperate'.

In his account of the palaeoenvironments of the south-western Cape and adjacent regions, Deacon (1979, table 1) recorded that the Miocene was characterized by an 'alternation between dominance by tropical palm and temperate vegetation', while during the Pliocene 'ancestral fynbos communities' were established. The evidence for these changes comes from fossil pollens studied by Coetzee (1978), who found that there was a warm phase in the region during the late Miocene when the vegetation was palm-dominated. Coetzee dated this phase to 8 Ma, but since it immediately preceded the terminal Miocene temperate phase associated with the Antarctic glacial maximum, it could have lasted to about 6 Ma. Palms and a casuarina apparently persisted through the terminal Miocene cool phase (Coetzee's Pollen Zone Lvi), into the Pliocene (Pollen Zone Lvii), when species typical of the fynbos make their first strong appearance. Consequently, it is possible that even though temperatures were no longer favourable, vestiges of a pre-existing monsoonal vegetation were still in evidence at Langebaanweg when the QSM and PPM were being deposited.

Axelrod & Raven (1978: fig. 6C), following Greenway (1970), indicate that during the latter half of the Miocene (i.e. c. 15–7 Ma) the south-western Cape was an area of 'subtropical forest' bounded a little to the north of Langebaanweg by 'sclerophyll vegetation'. During the period of environmental transition that followed, the forest was replaced by the sclerophyll vegetation. The displacement of the forests was evidently a gradual process which was still under way at the time that the QSM and PPM were being laid down.

It seems then that the main fossiliferous deposits of 'E' Quarry date from a period of transition, when climate, vegetation and fauna were in the process of change. These sometimes astonishingly rich fossiliferous deposits represent a period when a previously hospitable environment was undergoing a marked change for the worse. It was colder and drier, perhaps with rainfall tending towards a winter rather than summer peak, but in any case with a pronounced dry season; the vegetation was changing from forests or woodlands to more open types (fynbos and grassland), while there was a corresponding change amongst the terrestrial vertebrates, with open-country forms making a strong appearance.

The fynbos of the south-western Cape, in contrast to some other vegetation regions in Africa, is a less favourable habitat for larger mammals, and although the situation was to vary in response to changing environmental conditions during the Pleistocene (Hendey 1974a; Klein 1980), the environmen-

tal deterioration early in the Pliocene brought to an end the period when mammals perhaps enjoyed their greatest success in this region. The Varswater Formation provides the final and, indeed, only local evidence of this period.

The inferred habitat preferences of many of the 'E' Quarry taxa were given earlier (see pp. 45–53). The habitats of invertebrates tend to be very specific, and the 'E' Quarry species were invaluable in determining the depositional environments of the horizons in which they occur. As a general rule, vertebrates are less useful in this repect, although they are usually indicative of the major habitat types, namely, marine, fresh water and terrestrial. For example, representatives of the marine environment include sharks, certain birds, the seal, and cetaceans; freshwater taxa include the otter and the hippopotamus. The majority of the vertebrates are, however, terrestrial forms, and it is this group that will be dealt with here, since some provide an additional insight into the nature of the environment at the time that the Varswater Formation was laid down.

Amongst the herbivorous mammals both woodland species (browsers) and grassland species (grazers) occur. While the former predominate in terms of the number of species, grazers were more commonly represented at certain levels in the succession, or areas within the mine, evidently because of the taphonomic factors in operation. For example the alcelaphines (*Damalacra neanica* and *D. acalla*), which were undoubtedly grazers although relatively primitive representatives of their group, were the most commonly occurring of the larger mammals in the bed 3aS channel deposits of the PPM.

Before analysing the significance of faunal representation at any given level or area, it would be desirable if minimum numbers of individuals were determined. This has yet to be done because in many instances assemblages are very large and the sorting of body parts and identification of taxa represented is incomplete. Nevertheless, some patterns of representation are already obvious.

It was stated elsewhere (Hendey 1980: 56) that the remains of certain woodland species were incorporated in the Varswater Formation with increasing frequency as deposition progressed. The example cited was that of the giraffids, *Sivatherium*, *Palaeotragus*, and *Giraffa*. Conversely, the grazing rhinoceros *Ceratotherium* is represented in decreasing numbers.

This was interpreted as indicating that either woodlands were an increasingly widespread habitat in the vicinity, or that taphonomic factors were such that the remains of large woodland species were incorporated in the deposits in increasing numbers, while those of a large grazer correspondingly decreased. The former alternative is less likely in view of the representation of other grazers. These include the alcelaphines, *Damalacra neanica* and *D. acalla*, which are common in the higher levels (beds 3aS and 3aN), but very rare lower down (QSM). If grasslands were, indeed, giving way to woodlands, then the alcelaphines would also have been represented in diminishing numbers.

It may, in fact, have been the reverse situation that led to the observed representation of woodland–grassland species, that is, a diminution of woodlands in the area. The deteriorating local environment probably caused wood-

lands to be increasingly confined to the immediate vicinity of the river, thus restricting the habitat available to browsing species. Such animals would then have been increasingly hard-pressed in exploiting the diminishing food resources, with an increase in mortality caused by starvation being likely. In addition, it is possible that as the rainfall pattern was changing from a summer to winter maximum, it became more irregular and perhaps even diminished. Droughts might, therefore, have been an added hardship confronting the fauna.

There is evidence that at least some of the 'E' Quarry browsers were ill-adapted to prevailing conditions by bed 3aN times. For example, teeth of *Sivatherium* from this level sometimes exhibit hypoplasia of the enamel (fig.15)

Fig. 15. A–C. Incisors of *Sivatherium hendeyi* from the PPM 3aN (unnumbered Dump 10 specimens), with hypoplasia of the enamel. D. A healthy specimen.

This condition results from disturbances in the formation of the enamel matrix during development of the teeth, and is a positive indication of ill-health in the immature individual (Scott & Symons 1974). The aetiology in the case of the bed 3aN *Sivatherium* is not known, but a nutritional inadequacy is most likely. Such inadequacies could be caused by reduced food resources.

A second dental abnormality observed amongst bed 3aN browsers, is irregular and excessive wear of teeth. Although this was observed in several of the bovid species, it is most common in the teeth of the reduncines and/or tragelaphines. There are problems in distinguishing the teeth of these animals (see below), but it is virtually certain that the abnormal bed 3aN specimens belong to the reduncines (mostly *Kobus subdolus*, but some *Kobus* sp. B), the

species most commonly represented by easily distinguishable horn-cores. Abnormal wear on the teeth (Fig. 16) is reminiscent of that which is often found in zoo animals that have been provided with inappropriate food. For example, abrasive food such as hay, which is suitable only for hypsodont grazers, causes excessive and irregular wear on the teeth of browsers. Living reduncines are grazers, but the 'E' Quarry species have teeth resembling those of the browsing tragelaphines (Gentry 1980: 255–256). The implication is that the bed 3aN reduncines were browsers that were including in their diet an abrasive food (probably grasses) to which they were ill-adapted.

Indications are, therefore, that by bed 3aN times at least some, and perhaps all, the browsing herbivores in the fauna were under stress, with mortality probably being higher than usual. Thus, it could have been the diminution rather than an increase in woodland habitats that led to the increased number of browsers being incorporated into the accumulating 'E' Quarry deposits.

It has previously been postulated that rainfall at that time was strongly seasonal and that the fossiliferous channel deposits of beds 3aS and 3aN represent flood-season accumulations (e.g. Hendey 1980: 60–62). Conversely, the subaerially accumulated fossils of the QSM accumulated during the dry season (Hendey 1976a: 223–225). These conclusions are based on the nature of the deposits and the incorporated fossils.

For example, burnt bone is a not uncommon element of the QSM and PPM assemblages, indicating that vegetation and/or peat fires were a feature of the area at the time of their deposition (Hendey 1980: 66–67). Since hominid activity can be excluded as a possible cause of fires, as can volcanic activity and

Fig. 16. Reduncinae upper and lower molars from the PPM 3aN (unnumbered Dump 10 specimens), showing abnormal and excessive wear.

rock falls, it is most likely that fires were started by lightning. Such fires could be expected only if a pronounced, and perhaps prolonged, dry season had left the vegetation and peat deposits desiccated and inflammable. These fires must have placed the fauna under additional stress. Firstly, animals trapped in the fires would be injured or killed. This would apply especially in the case of slow-moving forms, such as tortoises, and this could account for the large numbers of tortoises found in the QSM, with its component of fossils accumulated subaerially during the dry season (see above). Secondly, fires would have further reduced the food supply available to herbivores, aggravating a starvation problem caused by a deteriorating environment, and the drought which preceded the first thunderstorms of the rainy season.

Lightning as the cause of fires is itself of palaeoenvironmental interest. Under existing climatic conditions thunderstorms occur in the south-western Cape only rarely ('nearly five occasions per year'—Schulze 1965: 313), and although lightning is known to cause fires in this region, such fires are infrequent, especially in the coastal areas (Kruger 1979). On the other hand, since thunderstorms are a characteristic accompaniment of strong solar heating, 'lightning is about ten times more frequent' in summer-rainfall regions (Kruger 1979, quoting Kröninger 1978). This may be further evidence for summer rather than winter rainfall in the Langebaanweg area during the early Pliocene.

Another possible effect of fires and the consequent reduction in vegetation cover at this time was the exposure of the unconsolidated sediments of the region to erosion at the onset of the wet season. This would account for the large volumes of sediment carried by the river and deposited at its mouth, so building up the Varswater Formation. In addition, there was probably an increased rainfall run-off from the devegetated areas and, consequently, an increase in the volume and duration of flooding. The devastating effects of the floods would, therefore, have been intensified.

There is now some additional evidence to support the hypothesis of seasonal deposition in the PPM during flood periods. A preliminary analysis of a sample of *Sivatherium* teeth from bed 3aN suggests that it represents a 'catastrophic' rather than 'atritional' mortality (see Voorhies 1969: 46, pl. 13 (figs 1–2)). There is also a suggestion that the material in this sample was accumulated during a restricted period of the year. Since it is abundantly clear that the bed 3aN *Sivatherium* specimens were deposited in a river channel, it is almost certain that they reflect a flood-season accumulation.

The situation that resulted in many of the fossils being incorporated in the QSM and PPM is summed up below.

During the dry season terrestrial vertebrates would tend to concentrate in the immediate vicinity of the river, including the now exposed QSM floodplain, where fresh water in the generally sandy region was probably most readily available. The area adjacent to the floodplain was probably the one to which woodlands were largely confined, and was therefore the main habitat available to browsing herbivores. Towards the end of each dry season the shortage of

food for herbivores might have become acute, with fires caused by electrical storms further reducing available supplies. The fires probably killed many animals, and might have caused others to drown when they sought refuge in the river. Most affected would have been slow-moving non-swimmers such as tortoises, which are abundantly represented in the QSM.

The first heavy rains of the wet season would cause flooding of the river. If the rains fell inland and not locally, the flooding may have caught animals concentrated on the floodplain unawares and swept them downstream to be deposited at its mouth, which was then in the vicinity of the present 'E' Quarry. Animals weakened by starvation or injured by fires were less likely to escape the flooding than healthy animals. In addition to animals drowned in the flood, the river would have carried with it remains of the animals that had previously died on the floodplain. The arrival at the river mouth of large numbers of carcasses of terrestrial vertebrates must have attracted aquatic carnivores such as seals and sharks to the area, while carcasses stranded on the river-banks would have attracted terrestrial scavengers. Those that died had their remains added to the accumulating deposits.

The representation of animals in the QSM and PPM, the large numbers of individuals involved, and the condition of their remains are thus indicative of the deteriorating environment in the region during the early Pliocene. A comparison between the mammals represented then and in modern times indicates very clearly that the fauna of the region underwent a radical change in the intervening period. Evidently this change had already been initiated by the early Pliocene.

The period of deposition of the Varswater Formation was one of transition, with the local physiography, climate, vegetation and fauna all being in the process of change. Patterns established earlier during the Miocene were still in evidence, but those that were to characterize the Quaternary were already being established.

EVOLUTIONARY ASPECTS OF THE MAMMALIAN FAUNA

Dating as it does from the period near the Miocene–Pliocene boundary, it is to be expected that the fauna of the Varswater Formation would have characteristics of both the time that Kurtén (1971: 152) has termed the 'climax of the Age of Mammals' (i.e. the late Miocene), and the Quaternary, which is characterized by similarly spectacular faunas only in some tropical regions, and with progressively less diverse faunas in higher latitudes. The 'E' Quarry fauna is, indeed, of a transitional nature and, at least in terms of its mammals, it provides a record unparalleled in Africa of the final flowering of Tertiary life before the climatic instability and extremes of the Quaternary so drastically altered the character and composition of the continent's fauna.

The 'E' Quarry carnivores serve admirably to illustrate the transitional nature of the fauna. They include representatives of genera such as *Agriother-*

ium, *Plesiogulo* and *Enhydriodon*, which were characteristic of the late Tertiary over wide areas of Africa, Eurasia and North America. Similarly, the hyaenas have previously been cited as an example of a group that had maintained a pattern of representation established during the late Miocene, and which contrasted with that during the Quaternary when the family was less diverse and individual species were more highly specialized (Hendey 1978c). The larger felids from 'E' Quarry are all sabre-toothed forms, and although such forms had a long subsequent history, they were never again to predominate as they did during the late Tertiary. By contrast, the mongooses of the early Pliocene were then only in the early stages of their radiation, which was to reach a climax during the Quaternary (Hendey 1974b).

Perhaps the best single example of a species intermediate between generalized Miocene forms and highly specialized Quaternary ones was not a terrestrial species but the seal, *Homiphoca capensis* (Hendey & Repenning 1972; De Muizon & Hendey 1980). In this instance the intermediate character could be fully documented, since *H. capensis* is very well represented, and there are closely related forms still living which are both generalized (monk seals) and specialized (Antarctic seals).

The 'E' Quarry carnivores also include early ancestors of species that were to become characteristic of later carnivore faunas. For example, *Hyaena abronia* and *Mellivora benfieldi* are likely ancestors of *H. hyaena* and *M. capensis* respectively (Hendey 1978c, 1978d). It is, however, equally significant that ancestors of several important elements of the Quaternary carnivore fauna of Africa are not represented at 'E' Quarry. These elements are the lion (*Panthera leo*), leopard (*P. pardus*), cheetah (*Acinonyx jubatus*), spotted hyaena (*Crocuta crocuta*), hunting-dog (*Lycaon pictus*), and jackals (*Canis* spp). They are largely open-country carnivores, with the cursorial cheetah being a particularly good example of an animal evolved to meet the changing environmental conditions of the late Tertiary. The cheetah has no counterparts amongst the 'E' Quarry felids, although the fauna does include an early 'hunting-hyaena' (*Euryboas*), which was an ecological vicar of the cheetah during the late Pliocene and early Pleistocene.

While the evolution of specialized carnivores such as the lion, leopard, cheetah, spotted hyaena, and hunting-dog can be ascribed ultimately to the changing environment of the late Tertiary, the reasons for the subsequent success of generalized forms such as the jackals are less obvious. The ecological vicars of the jackals in the 'E' Quarry fauna were the civets (Hendey 1974a). At least in terms of their size and dentitions there was little difference between jackals and civets and it can be assumed that they had similar feeding-habits. However, the early Pliocene civets had relatively small brains (Fig. 17), and it is possible that in terms of sight, smell, and/or hearing they were inferior to jackals and were thus unable to compete with them successfully. The living African civet that survived this competition did so by becoming a nocturnal omnivore and coincidentally increasing its brain size.

Fig. 17. Dorsal, lateral and ventral views of a civet skull (SAM–PQ–L51590) from the PPM 3aN.

In the case of the marine vertebrates such as the seal, the changing characteristics manifested in late Tertiary lineages can also be ascribed to environmental factors, principally falling sea temperatures. The development of the nutrient-rich cold upwelling in the Benguela Current System resulted not only in an adaptation in *Homiphoca* to colder conditions, but also led to adaptations in the postcranial skeleton, which permitted the more pelagic way of life required to exploit the rich off-shore food resources, and those parts of the skull connected with feeding in order to deal with the pelagic foods.

The fact that the 'E' Quarry mammals date from a period when the fauna was adapting to changing conditions has contributed to the difficulties in identifying certain taxa. In such instances the differentiation of new lineages was in its early stages, as in the case of the civets and canids (see p. 55), and consequently the distinguishing characteristics, which were later to become unequivocal, were still only slight. Apart from the examples cited above, forms that resemble one another in many respects are included amongst the mongooses (Hendey 1974*a*, 1974*b*), hyaenas (Hendey 1978*c*), and bovids (Gentry 1980).

The diminution of forested or wooded environments was probably the most significant factor in bringing about change amongst the terrestrial mammals. This change was manifested by extinctions, by reducing the distribution of species, and by the evolution of new taxa that were better adapted to the changed environment. Large herbivorous species must have been most affected, while the viability of carnivores which depended on them as a source of food would have been placed in jeopardy. The large bear, *Agriotherium*, falls into the latter category (Hendey 1980; 69–72). Ultimately though, the entire fauna must have been affected to some extent.

A herbivore that became extinct without issue was the woodland boselaphine, *Mesembriportax* (or *Miotragocerus*) *acrae*. During the late Miocene, near relatives of this bovid had been amongst the most successful and widespread of their family in Eurasia, and perhaps also Africa. Apart from the living four-horned antelope (*Tetracerus quadricornis*) and nilgai (*Boselaphus tragocamelus*) of India, the 'E' Quarry boselaphine is probably the last recorded survivor of its group.

Much the same applies in the case of the okapi-like *Palaeotragus* cf. *germaini*. Palaeotragines were an important element in the late Miocene faunas of Eurasia and Africa, but the sole survivor of the group today is the rare *Okapia johnstoni*, which is confined to forests in equatorial Africa (Churcher 1978). The Pliocene and Pleistocene history of the Palaeotraginae is poorly documented, or perhaps misinterpreted, but 'E' Quarry is one relatively late occurrence where its presence is indisputable. It is, however, a rare element in the fauna, and by the early Pliocene the heyday of the subfamily was clearly past.

Sivatherium hendeyi is the most commonly occurring of the 'E' Quarry giraffids and, although the genus survived well into the Pleistocene in Africa, it

is nowhere as commonly represented as it is in 'E' Quarry. The group to which it belonged flourished in Eurasia, and perhaps also Africa, during the late Miocene, and 'E' Quarry may provide a record of its final flowering.

There are several instances where descendants of taxa recorded from 'E' Quarry, or later related forms, had adapted to changing conditions through altering their dietary preferences. Adaptations to grazing rather than browsing were already evident in the 'E' Quarry rhinoceros (*Ceratotherium praecox*) and alcelaphines (*Damalacra acalla* and *D. neanica*), and perhaps also the buffalo (*Simatherium demissum*), gazelle (*Gazella* sp.), and neotragine (*Raphicerus paralius*). *Notochoerus*, the warthog-like descendant of *Nyanzachoerus* (Cooke & Wilkinson 1978; Harris & White 1979), was subsequently to follow suit. The 'E' Quarry grazers were still relatively primitive members of their groups, and from the stocks that they represent were to arise the characteristic grazing species which flourished in Africa during the Quaternary.

Although it was vegetational change that had the major affect on the composition of the fauna, the related factors of rainfall and temperature must also have played a role. There can be little doubt that the 'E' Quarry fauna had its origins under tropical rather than temperate conditions, and, consequently, that adaptation to cooler conditions in the terminal Miocene and early Pliocene was required. Certain of the 'E' Quarry taxa, both mammals and non-mammals, have modern counterparts only in the warmer parts of Africa, and this suggests that ultimately they did not successfully adapt to the temperate conditions that prevailed in the south-western Cape after the late Miocene. Such taxa include a snail (*Ceratophallus natalensis*), the parrots (gen. and spp not determined), the giraffe (*Giraffa* sp.), the 'okapi' (*Palaeotragus* cf. *germaini*), and the reduncines (*Kobus* spp). It is possible that even by the early Pliocene, falling temperatures had influenced the composition of the fauna, with some tropical forms having already become extinct locally (see p. 89).

The effects of a change in rainfall are not obvious. If there was indeed a change from summer to winter rainfall, this would not necessarily have had an advserse effect on the mammals, although there might have been a reaction to a lowering of rainfall and/or a lengthening of the dry season.

In assessing evolutionary aspects of the 'E' Quarry fauna, account must be taken of events elsewhere, since this fauna was as much influenced by them as it was by local environmental changes.

In the Old World the record of terrestrial life during the late Miocene is well documented in parts of Europe and Asia, but in Africa the fossil record for this period is poor. It is, however, safe to assume from the little that is known, and from earlier and later records, that Africa during the late Miocene was as richly endowed faunally as Eurasia. Its fauna was comprised of both endemic lineages and ones that had their origins in Eurasia and North America.

After a long period early in the Tertiary when it was isolated from other continents by seas and oceans, Africa–Arabia was joined to south-western Asia early in the Miocene (Berggren & Van Couvering 1974). This event had a

profound impact on the faunas of both Africa and Eurasia. Whereas earlier in the Tertiary faunal interchange had been limited to 'sweepstakes routes' (*sensu* Simpson 1967), or 'Noah's Arks' (*sensu* McKenna 1973), the early Miocene saw the opening of 'corridor routes' which allowed the first free faunal interchange in perhaps 40 million years. African emigrants to Eurasia included primates and proboscideans, while an array of Eurasian taxa, including carnivores and perissodactyls, made their appearance in Africa (Maglio 1978).

Thereafter, the corridors between Eurasia and Africa were restricted or closed intermittently, and Africa's faunal history was punctuated by periods of isolation which were interrupted by new periods of immigration. In spite of the closer connection with Eurasia, immigrant lineages to Africa evolved taxa that were usually in some respects distinct from their Eurasian counterparts, and they, together with representatives of endemic lineages, gave the African fauna a largely distinctive character throughout the later Cenozoic.

The 'E' Quarry fauna, and others of late Miocene and early Pliocene age elsewhere in Africa, provide evidence for a period of immigration from Eurasia during the late Miocene. Conversely, there is evidence from Eurasia of the immigration of African mammals at this time. For example, Azzaroli (1975: 69) concluded that it is 'firmly established that interchange of terrestrial mammals between southern and northern shores of the Mediterranean took place some time around 6,5 m.y. ago or shortly later'.

Amongst those mammals from 'E' Quarry with a late Miocene Eurasian connection is the bear, *Agriotherium africanum* (Hendey 1980). A slightly earlier member of the lineage which includes *A. africanum* is recorded from *c.* 6 Ma deposits at Sahabi in Libya (Boaz *et al.* 1979), and it is likely that the earliest African representative of the group entered the continent about that time or slightly earlier, that is, during the *c.* 6,5 Ma faunal interchange recorded by Azzaroli (1975). Other likely immigrants to Africa at this time are the hyaenids, *Ictitherium*, *Palhyaena* (=*Hyaena*), and *Hyaenictitherium*; the wolverine, *Plesiogulo*; and the false sabre-toothed cat, *Dinofelis*, the latter being a descendant of Eurasian *Metailurus* (see Hendey 1974*a*, 1978*c*, 1978*d*, 1980). The largest of the 'E' Quarry hyaenids, '*Adcrocuta*' *australis*, was previously thought to be included in this category, having been descended from Eurasian *Adcrocuta eximia*, but it now seems likely that these two species had a common ancestor in an earlier African percrocuta.

Immigrants amongst the herbivores are less obvious. One possiblility is the boselaphine, *Mesembriportax* (or *Miotragocerus*) *acrae*. According to one interpretation, this species was descended from the widespread *Miotragocerus* of the Eurasian late Miocene, again with an intermediate form being recorded from Sahabi (Thomas 1979). On the other hand, it may represent an endemic African lineage that had its origins with the middle Miocene *Protragocerus*, and which evolved in parallel with Eurasian *Miotragocerus* (Gentry 1974, 1980).

It is significant that descendants of late Miocene immigrants are most obvious amongst the larger Carnivora. Such animals are less affected than

herbivores by environmental factors, and are thus capable of more rapid dispersal, while individual species tend to have wider distributions. Consequently, descendants of late Miocene immigrant carnivores to Africa might have become established in the far south of the continent sooner than their herbivorous counterparts. The more slowly dispersed herbivores are also likely to undergo more rapid evolutionary changes as they adapted to new environmental conditions, and their relationships to pre-existing forms may therefore be more difficult to determine.

Not all the ancestors of Eurasian immigrants represented in the 'E' Quarry fauna reached Africa late in the Miocene. One obvious exception is *Hipparion*, whose appearance in Africa dates back about 12,5 Ma (Churcher & Richardson 1978). By the end of the Miocene endemic African species of *Hipparion* had evolved (Churcher & Richardson 1978). The Langebaanweg *Hipparion* is of particular interest, since it is recorded from all the main fossil-bearing horizons of the Varswater Formation, as well as from younger deposits. At least one lineage (*H.* cf. *baardi–H. baardi*) is represented which is distinct not only from its counterparts in Eurasia, but also those elsewhere in Africa. The same apparently applies in the case of the two alcelaphines from 'E' Quarry, one of which has a descendant form in Baard's Quarry, although in this instance the origins of the group are still obscure (Gentry 1980).

Another of the 'E' Quarry species that might have been descended from an Eurasian middle Miocene species is the peccary, *Pecarichoerus? africanus*. Previously a connection with the Asian *Pecarichoerus orientalis* was suggested (Hendey 1976b), but a recently described peccary from the late Vindobonian of Spain, *Barberahyus castellensis* (Golpe-Posse 1977), is remarkably similar to the 'E' Quarry species and they may have a close phylogenetic relationship, with descendants of the Spanish form having entered Africa at the same time as *Hipparion*.

In interpreting the evolutionary history of Varswater Formation mammals it is therefore necessary to take into account the following possibilities:

1. Species represent lineages endemic to Africa.
2. Species represent lineages of Eurasiatic origin, and with a long history in Africa.
3. Species represent lineages of Eurasiatic origin, and with only a short history in Africa.
4. Species represent lineages of African or Eurasian origin, but which are endemic to the southerly parts of the continent.

In addition, account must be taken of the possibilities that certain lineages represented elsewhere in Africa failed to make an appearance in the Langebaanweg area, only arrived there long after they were established further north, and became extinct there earlier, or survived later, than they did further north.

The matter of locally endemic species, non-arrivals, late arrivals, early extinctions, and late ·survivors during any given period depends on local

environmental conditions, as well as the degree to which the south-western Cape, or southern Africa, was zoogeographically isolated from regions further north. The potential for isolation of the south-western Cape, largely by a barrier of aridity or semi-aridity, has already been established (Hendey 1974a; 14–19), although the degree of isolation at various times in the past is difficult or impossible to determine. This applies particularly to pre-Quaternary times, when African environments were very different from those of the present, and when the fossil record is generally poor.

The fact that 'E' Quarry species such as *Hipparion* cf. *baardi* and the two alcelaphines are, or may be, different from contemporary counterparts further north in Africa, suggests that the south-western Cape, or an even larger area of southern Africa, had been zoogeographically isolated some time during the late Miocene. On the other hand, this isolation could not have been complete, or had broken down very late in the Miocene, since there evidently had been some immigration of taxa shortly before deposition of the QSM and PPM. Such taxa include *Agriotherium* and the others referred to above.

Since the Varswater Formation was laid down over an appreciable period, it is also possible that during this period some species arrived in the area as immigrants, while others became extinct. However, it may not be possible to determine that this actually happened. The simple fact that certain species are not recorded low in the sequence does not necessarily mean that they were not present in the area. In other words, the first appearance of a species in the sequence was not necessarily coincident with its first appearance in the region. Conversely, the presence of certain taxa low in the sequence, and their absence higher up, is not necessarily indicative of their extinction. Both sampling inadequacies and taphonomic factors are potential biases in the 'E' Quarry record.

Sampling inadequacies is the less serious problem, since the sample sizes from the QSM, bed 3aS, and bed 3aN are large. Nevertheless, past experiences at this locality have shown that it is a factor that cannot be dismissed. For example, it was once thought that porcupines had not been an element of the fauna (Hendey 1974a), but remains of a single individual were subsequently found in the QSM (Hendey 1976a), and since then fragmentary remains of a second species have turned up on several occasions in beds 3aS and 3aN.

The problem with taphonomic factors is that the environments of deposition of the various elements in the succession vary, and it is obvious that taxa represented in one (e.g. river floodplain) may differ from those in another (e.g. river channel).

The QSM assemblage largely represents the remains of animals that lived and died in the immediate vicinity, whereas the beds 3aS and 3aN assemblages are largely comprised of animal remains washed in by the river from elsewhere. Consequently, the presence of species in these two sets of deposits simply reflects the opportunity for their remains to reach their points of deposition, and may have nothing to do with their presence or absence in the region.

Individual taxa must, however, be assessed separately. For example, the fact that hippos are not recorded from the QSM may be due to the lack of exposures of those deposits where their remains were most likely to be preserved, that is, those of the main river channel of that time. However, even in the recorded channel deposits hippos are unequally represented. They were extremely rare in bed 3aS, whereas they were much more common in bed 3aN. It is thus possible that the representation of this animal in the 'E' Quarry sequence is a true reflection of its initial absence (i.e. in QSM times), and its subsequent presence in increasing numbers (i.e. in beds 3aS and 3aN).

The occurrence of the giant pig, *Nyanzachoerus*, is in curious contrast to that of the hippo. *Nyanzachoerus* occurs quite commonly in the QSM, *N.* cf. *pattersoni* being one of the characteristic species of this horizon. This species may also be present in bed 3aS, although it is extremely rare. A second species, *N.* cf. *jaegeri*, is definitely recorded from bed 3aS, although it, too, is uncommon. However, neither species, nor any other pig, is recorded from bed 3aN. This creates the impression that *Nyanzachoerus* was 'replaced' locally by the hippo. There is, however, no evidence from elsewhere that hippos and *Nyanzachoerus* were mutually exclusive taxa, although they might well have competed for a common food source.

The situation in respect of these animals at Langebaanweg might have differed from that in areas where they did co-exist. Since the local environment was deteriorating during the early Pliocene, it is possible that competition between hippos and *Nyanzachoerus* for diminishing food resources was critical enough to cause the extinction of the latter. Thus the record of hippos in bed 3aS may, indeed, coincide with the first appearance of these animals in the Langebaanweg area and the initiation of competition with *Nyanzachoerus*, the latter process being concluded in the favour of the hippos by the time that bed 3aN was deposited. Alternatively, the two forms might have co-existed throughout the period of deposition of the QSM and bed 3aS, with the displacement process being more gradual. The first of these alternatives is perhaps the more likely in view of the observed relative abundance of the two forms.

One of the more intriguing features of the QSM and PPM faunas is the extreme rarity of primates in the former and their complete absence in the latter. Of the many thousands of mammalian teeth recovered to date, there are only two specimens from the QSM identified as primate, while there are no primate bones amongst the far more numerous identified postcranial remains from the QSM and PPM. Primates are clearly grossly under-represented in the 'E' Quarry fauna, given its location in Africa, the great number and variety of mammals recorded, and the vast number of specimens already collected and identified. In older and broadly contemporary faunas elsewhere in Africa, and in southern Eurasia, both terrestrial and arboreal primates are represented, sometimes in appreciable numbers and variety and often in assemblages far smaller than that from 'E' Quarry.

It was suggested elsewhere that the location of Langebaanweg on the coast

in the far south of the continent might have had a bearing on the under-representation of primates (Hendey 1976a: 234). The coastal situation is unlikely to have been significant, since primates are not necessarily averse to this kind of environment, either now or in the past. For example, the broadly contemporary fauna from Montpellier, which was accumulated in a similar environment, includes primates (see below).

The situation of Langebaanweg at nearly 34°S may be a more significant factor. Over 80 per cent of Africa's non-hominid primates occur in low latitudes, between 15°N and 15°S (see distribution maps in Dorst & Dandelot 1970), and are thus most characteristic of the hot tropical regions. In the warm-temperate south-western Cape there is only one non-hominid primate recorded, which is about 2 per cent of the total in the Ethiopian Region. This species is the chacma baboon, *Papio ursinus*. A monkey (probably *Cercopithecus*) is tentatively recorded on the basis of early historical records. The Pleistocene fossil record for the south-western Cape is comparatively good, but once again only one non-hominid primate is recorded, i.e. the baboon, *Theropithecus oswaldi*, from the middle Pleistocene of Elandsfontein. Clearly, the frequency in the occurrence of primates can be correlated with latitude, and, consequently, also with temperature.

However, the lower temperatures of higher latitudes do not necessarily directly limit the occurrence of primates. Instead, they have the effect of limiting the food resources available to essentially herbivorous primates. Tropical regions remain productive in terms of such food resources throughout the year, but in temperate regions they are readily available only during summer. Consequently, although the vegetation at Langebaanweg during the early Pliocene was such that the occurrence of both terrestrial and arboreal primates might have been expected, winter temperatures were probably already too low to have maintained adequate food supplies for most primates. This order may, therefore, be included in the hypothetical group of animals that became extinct in the south-western Cape earlier than elsewhere (see p. 83).

It is worth noting that primates were still present in contemporary faunas of comparable latitudes in the Northern hemisphere. This is readily explained by the fact that the existing zonality in world climates had yet to be established. The glaciation of the Arctic lagged behind that of Antarctica, and it was not until about 3 Ma that the situation in the two hemispheres was more or less equalized.

The above theory implies that primates were still present in the far south of the continent during the warmer period in the late Miocene and earlier. However, although the Miocene mammal record for southern Africa is very poor, it may again be significant that this record includes no primates. Only one Miocene occurrence is presently known where the assemblage is sufficiently large for primates to have been expected. It is from Arrisdrift in the southern Namib desert, and in this instance it was suggested that zoogeographic barriers between east and southern Africa might have impeded the southward dispersal of primates (Hendey 1978b: 35).

Other notable absentees from the 'E' Quarry fauna are the Deinother-iidae, Chalicotheriidae, and, amongst the non-mammals, the Crocodilia. Pro-boscideans are a comparatively rare element in this fauna, and the absence of a deinothere may therefore reflect a sampling deficiency. The same may apply in the case of the chalicothere, an animal that was uncommon elsewhere in Afriica as well. The situation in respect of the Crocodilia is likely to be different, since wherever these animals are present they are likely to be well represented at least by isolated teeth and scutes, if not by other skull parts and postcranial bones. Crocodiles have not been recorded from any other south-western Cape deposits either, and their absence is probably due to the relatively low temper-atures in local aquatic environments in post-Miocene times.

Both deinothere and crocodile are recorded from the early middle Miocene deposits at Arrisdrift, 500 km to the north, so they, like primates, might have had their ranges restricted by falling temperatures in the far south of the continent during the late Miocene and early Pliocene.

Although the 'E' Quarry fauna includes Eurasian immigrants, it was dominated by taxa that were, and, in some cases, still are, characteristically 'African'. These include groups such as the Macroscelididae, Chrysochloridae, Tubulidentata, Proboscidea, Hyracoidea, and certain tribes of Bovidae.

The 'African' character of this fauna is clearly manifested by a comparison with the broadly contemporary Montpellier fauna (Table 9). Apart from these faunas being of comparable age, they are from similar coastal situations. In their overall composition the faunas of 'E' Quarry and Montpellier are remark-ably alike, comprising of a similar array of carnivores, proboscideans, perisso-dactyls, artiodactyls, cetaceans, and some smaller mammals. The latter are under-represented at Montpellier probably because of sampling deficiences, while the under-representation of primates in 'E' Quarry is ascribed to the climatic factors discussed above.

In spite of their overall similarities, the two faunas are taxonomically distinct, the differences being mainly at generic and specific level. Conspecificity, or very close relationship, is largely confined to the Carnivora, for reasons discussed earlier (see p. 84), but even in this group there are obvious differences.

The most striking and unexpected of these differences is the absence of hyaenas at Montpellier. Hyaenas are well represented in Europe at localities of late Miocene and Pleistocene age, and they are also common in 'E' Quarry. Their comparative rarity (or absence) at European localities of early Pliocene age has yet to be satisfactorily explained. Smaller viverrids are also not recorded at Montpellier, but otherwise differences from 'E' Quarry carnivores are at generic or specific level.

For example, the badgers represent the genera that are still characteristic of the continents concerned (i.e. *Mellivora* in Africa, *Meles* in Europe). Similarly, the seals, both of which belong to the subfamily Monachinae, are most closely related to taxa that are still found in geographical proximity (i.e. *Homiphoca* to Antarctic Lobodontini, *Pristiphoca* to Mediterranean *Monachus monachus*).

TABLE 9

The mammalian faunas of the Varswater Formation (QSM and PPM), Langebaanweg, and the Pliocene deposits at Montpellier, France.

	LANGEBAANWEG	MONTPELLIER*
Insectivora and Chiroptera	Present	Not recorded
Primates	1 species	3 species
Pholidota and Tubulidentata	Present	Not recorded
Carnivora		
Canidae . . .	2 species	Not recorded
Ursidae . . .	*Agriotherium africanum* (aff. *insigne*)	*Agriotherium insigne*
Mustelidae . .	*Plesiogulo monspessulanus* *Mellivora benfieldi* *Enhydriodon africanus*	*Plesiogulo monspessulanus* *Meles gennevauxi* *Lutra affinis*
Phocidae . .	*Homiphoca capensis*	*Pristiphoca occitana*
Viverridae . .	*'Viverra' leakeyi* Viverrinae sp. B *Genetta* and Herpestinae	*Viverra* aff. *pepratxi* Not recorded
Hyaenidae . .	Several species	Not recorded
Felidae . .	Machairodontinae (2 spp) *Felis* aff. *issiodorensis* (? aff. *christoli*) Other Felinae (3 spp)	Machairodontinae (1 sp.) *Felis christoli* Not recorded
Proboscidea . .	*Mammuthus subplanifrons* *Anancus* sp.	*Mastodon arvernensis*
Hyracoidea . .	*Procavia* cf. *antiqua*	*Pliohyrax occidentalis*
Perissodactyla		
Equidae .	*Hipparion* cf. *baardi*	*Hipparion crassum*
Rhinocerotidae .	*Ceratotherium praecox*	*Dicerorhinus megarhinus*
Tapiridae . .	Not recorded	*Tapirus arvernensis*
Artiodactyla		
Tayassuidae . .	1 species	Not recorded
Suidae . . .	*Nyanzachoerus* (2 spp)	*Sus arvernensis*
Hippopotamidae .	1 species	Not recorded
Giraffidae . .	3 species	Not recorded
Cervidae . .	Not recorded	3 species
Bovidae . .	12 species, including a *Gazella* sp.	2 or 3 species, including a *Gazella* sp.
Lagomorpha . .	*Pronolagus* sp.	*Prolagus* sp.
Rodentia . .	Many species	1 species
Cetacea . . .	Several species	Several species

*Anonymous 1975

Amongst the non-carnivores, giraffids and bovids are the predominant ungulates in 'E' Quarry, whereas at Montpellier giraffids are absent (or not recorded), and cervids are present in addition to bovids. *Hipparion* is recorded at both localities. The combinations of Bovidae–Giraffidae–Equidae in 'E' Quarry and Cervidae–Bovidae–Equidae at Montpellier are still characteristic of the continents concerned.

DATING OF THE LANGEBAANWEG SUCCESSION

One of the most persistent problems pertaining to the Varswater Formation is that of its age. As is frequently the case in southern Africa with deposits of late Cenozoic age, only indirect dating methods can be used. The situation is, however, exceptional in that in this instance faunal, botanical and geological evidence is actually or potentially available for relative dating purposes. The present study has clarified the dating problem.

Hitherto dating has depended largely on the fossil mammals of the Varswater Formation. Initially these fossils were thought to be of early Pleistocene age (e.g. Singer 1961; Boné & Singer 1965; Hendey 1969, 1970a), but subsequently it was suggested that the formation included both Pliocene and Pleistocene elements (Hendey 1970b). This is, indeed, the case with the fossil assemblage from Baard's Quarry (Hendey 1978a), but the Varswater Formation in 'E' Quarry is entirely of late Tertiary age. This was established with the realization that geological evidence had been misinterpreted, that some of the mammalian taxa represented had been misidentified, and that the provenance of an *Equus* tooth had been incorrectly recorded (Hendey 1972b). Thereafter, the most widely accepted age estimate was early Pliocene (c. 4–5 Ma) (e.g. Hendey 1973, 1974a). Instead of resolving the issue, more recent faunal studies have provided contradictory dating evidence and have also indicated that deposition of the Varswater Formation took place over a prolonged period (e.g. Hendey 1976a, 1978d, 1980). As a result, when referring to the age of this formation it has been the practice to give only the outside age limits, which are 7 and 3,5 Ma. These limits include the terminal Miocene as well as the early Pliocene.

The principal difficulty with faunal dating has been that broadly contemporary faunas elsewhere in Africa, some of which are securely dated by absolute age determinations, are not well known. Consequently, the basis for comparison is far less than the lengthy 'E' Quarry faunal list would suggest. In addition, the location of Langebaanweg near the southern continental extremity raises the problem of regional peculiarities in the fauna of the kind discussed above (see pp. 85–89).

In that discussion the 'E' Quarry hippo was used as an example to illustrate a point, and it can be used again to indicate the kind of difficulties that arise in faunal dating. The fossil record of Hippopotamidae in east Africa is good, and the evolutionary history of the family is well understood (Coryndon 1978). Hippos are not the best mammals to use for relative dating purposes, since they are conservative animals in an evolutionary sense, and are difficult to identify

to species level on the basis of fragmentary material. Nevertheless, they may serve as age indicators in the case of faunas such as the one from 'E' Quarry.

It was suggested earlier that hippos might have made their appearance in the Langebaanweg area only during the period of deposition of bed 3aS (or shortly before). Hippos are first recorded in east Africa as early as 10 Ma (Coryndon 1978), but it would be unwise to conclude that their first appearance there coincided with their appearance in the Varswater Formation. It is much more likely that environmental factors retarded the southward dispersal of this water-demanding animal, perhaps for an appreciable period. Hippos may thus be an example where geography is a complicating factor when they are used for relative dating purposes.

A contrasting example of a herbivore noted for its rapid dispersal and utility in faunal dating is that of *Hipparion*, the three-toed horse that first made its appearance in Africa at about 12,5 Ma, and which survived on this continent well into the Pleistocene (Churcher & Richardson 1978). Again there is a complicating factor with the Langebaanweg representatives of this genus. The most commonly occurring of the 'E' Quarry species is *Hipparion* cf. *baardi*, which evidently belongs on a lineage endemic to the more southerly parts of Africa, and comparisons with broadly contemporaneous *Hipparion* elsewhere in Africa, therefore, provide little evidence of their likely relative age.

The Langebaanweg *Hipparion* has, however, provided useful relative age information on deposits occurring in the immediate vicinity. For example, the GM *H.* cf. *primigenium* is consistent with the late Miocene date for this horizon deduced on other evidence (see p. 23). Another species, *H.* cf. *namaquense*, is known only from the uppermost levels of the Varswater Formation, and may even come from overlying deposits (Hendey 1976a; Hooijer 1976). Finally, the Baard's Quarry *H. baardi*, which is now also recorded from the Anyskop terrestrial deposits, is clearly distinct from the 'E' Quarry *H.* cf. *baardi*, and suggests a younger date for the deposits in which it occurs (Hendy 1978a; see also p. 38).

Bearing in mind the difficulties in long-range correlations suggested by the hippo and *Hipparion*, and the other potential regional peculiarities discussed earlier, it is evident that in faunal dating of the Varswater Formation the following two factors are of the greatest significance:

1. The occurrence at more securely dated localities of species conspecific with ones occurring in 'E' Quarry.
2. The evolutionary state of 'E' Quarry taxa relative to those of related taxa from dated localities elsewhere.

Initially it was two species from the QSM that were at the core of the correlations indicating an early Pliocene age. They were the elephant, *Mammuthus subplanifrons*, and the pig, *Nyanzachoerus* cf. *pattersoni* (or *kanamensis*). A 5 Ma maximum age for the QSM was based on the belief that counterparts of

these two species in the Lothagam 1 fauna from Kenya were aged between 5 and 6 Ma (Patterson *et al.* 1970; Maglio 1973). Subsequently Hooijer & Maglio (1974: 4) concluded that this fauna 'may be somewhat older than [6 Ma, but] it is not likely to be much younger'. Behrensmeyer (1976: 167) noted that it is 'obviously important to think of the Lothagam 1 fauna as representative of a relatively long time span' and that 'the fauna from 1C may be somewhat younger than 6,0 m.y.' The base of the Lothagam sequence is underlain by volcanics dated at 8,3 Ma (Behrensmeyer 1976), which is, therefore, the absolute maximum age of the Lothagam fauna.

Although there is still uncertainty about the actual age of the Lothagam 1 fossils, there can be virtually no doubt that they pre-date those from the QSM, and, consequently, also those from beds 3aS and 3aN. The Lothagam 1 elephants (*Stegotetrabelodon orbus*, *Primelephas gomphotheroides*) and the pig (*Nyanzachoerus tulotus*) are more primitive than their counterparts from 'E' Quarry, as is an undescribed hyaenid from Lothagam 1.

On the other hand, the *c.* 4 Ma fauna from Kanapoi, 75 km south of Lothagam (Behrensmeyer 1976), is apparently younger than that from 'E' Quarry, although the evidence for this is more slender. An undescribed hyaenid from Kanapoi is certainly more advanced than its counterparts in the 'E' Quarry '*Hyaena* group' (see Hendey 1978c). The presence of the pig, *Notochoerus*, at Kanapoi and its absence in 'E' Quarry is also indicative of a younger age for the former. In addition, the QSM *Nyanzachoerus* cf. *pattersoni* is slightly more primitive than the *N. pattersoni* from Kanapoi in retaining P^1. The preceding evidence indicates that the age difference between the two faunas is of no great magnitude, an opinion supported by the fact that their elephants are in a comparable evolutionary state (Maglio 1973).

There is, however, a complication with the *Nyanzachoerus* cf. *jaegeri* from bed 3aS in 'E' Quarry. White & Harris (1977) and Harris & White (1979) have suggested that the relative stratigraphic positions of *N.* cf. *pattersoni* (or *kanamensis*) and *N.* cf. *jaegeri* in 'E' Quarry are evidence in support of their theory that the latter evolved from the former. According to their correlation the upper levels of the Varswater Formation (i.e. beds 3aS and 3aN) actually overlap with the Kanapoi Formation (Harris & White 1979, fig. 134). This conclusion is in conflict with the evidence that suggests that all of the Varswater Formation is older.*

The most positive indication of the earlier date for the Varswater Formation relative to the Kanapoi Formation comes from the hyaenids. The three 'E' Quarry species most closely related to the Kanapoi hyaenid are *Ictitherium preforfex*, *Hyaena abronia*, and *Hyaenictitherium namaquense*, all of which retain P_1 and M_2, teeth which the Kanapoi species has lost.

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* A recent examination of the 'E' Quarry *N.* cf. *jaegeri* by T. D. White has led him to believe that it represents a more primitive variety than the one from Kanapoi, and that the 'E' Quarry pigs are consistent with a 5 Ma date.

Correlation of the 'E' Quarry fossils with those from east African localities such as Lothagam and Kanapoi was recently further complicated by Gentry's (1980: 333) conclusion that 'the bovids best indicate an age of about 6 m.y. for the fauna'. The bovids thus suggest an age comparable to Lothagam 1, and appreciably older than Kanapoi. However, the bovids do not necessarily rule out a younger age, and at least in the case of the buffalo, *Simatherium demissum*, are consistent with such an age. Gentry (1980: 332) found that '*Parabos boodon*, which is at a comparable evolutionary level [to *S. demissum*, but] on a different lineage, comes from Perpignan, which is given an age of about 4,8 m.y.'

While the utility of groups such as the elephants, pigs, and bovids in faunal dating is undeniable, preference is here given to that of the carnivores. The environmental tolerance of these animals allows at least the larger species to disperse rapidly when the opportunity arises, with little or no evolutionary adaptation necessarily required, and with consequent wide distributions for individual species. This facilitates long-distance correlations. The post-Lothagam 1 and pre-Kanapoi age for the 'E' Quarry fauna indicated by the hyaenids is, therefore, regarded here as more acceptable than the conflicting evidence of the pigs and bovids, and the equivocal evidence of the elephants. The outside age limits of 3,5 and 7 Ma are thus reduced to 4 and 6 Ma, with a median estimate of 5 Ma applying.

The 'E' Quarry carnivores provide further evidence in support of the 5 Ma estimate. The recent study of the *Agriotherium* from this locality suggested that it is at a comparable evolutionary stage, or, in the case of the bed 3aN material, perhaps even slightly more advanced than the *Agriotherium* from Montpellier in France. Similarly, available materials of the *Plesiogulo* and a small *Felis* from the two localities are virtually indistinguishable. Other, more general similarities between the two faunas were referred to earlier (see p. 89, Table 9), and faunal evidence thus points to broad contemporaneity between the 'E' Quarry deposits and those of Pliocene age at Montpellier.

The latter were laid down during the marine transgression that terminated the Messinian salinity crisis and ushered in the Pliocene. It was this correlation that first suggested that deposits in the Langebaanweg area could be related to global phenomena of the late Tertiary, and which prompted the re-examination of the local succession, a process that was to culminate with the correlation with global sea-level changes (see pp. 12–18, Fig. 3, Table 2).

This correlation has placed the matter of the age of individual elements in the Langebaanweg succession in an entirely new light. Whereas previously even correlations with deposits and faunas elsewhere in Africa were generally tentative, there is now the potential for secure correlations with successions recorded from all the continents and oceans of the world. In addition, the Langebaanweg area could become the key to interpreting other late Tertiary strata in southern Africa, which have often proved difficult to date, and which have had obscure histories and relationships.

While the correlation of individual elements in the Langebaanweg succes-

sion with subdivisions of the late Tertiary epochs appears secure, the absolute or chronometric ages of these elements have yet to be precisely determined.

For example, although the QSM, PPM, and Anyskop marine deposits date from the early Pliocene transgression, there is as yet no consensus on the timing and duration of this event. On the basis of evidence from the Mediterranean Basin, Van Couvering et al. (1976) and Van Couvering & Berggren (1977) indicate that this transgression took place between 5,0 and 4,5 Ma, whereas Vail & Hardenbol (1979) indicate it as a rapid event that took place at 5,2 Ma. The essential difference between these interpretations concerns the dating of the Miocene–Pliocene boundary, which is taken respectively at 5,0 and 5,2 Ma, while there are also implications concerning the duration of the transgression.

Clearly, the dating of the Miocene–Pliocene boundary is a matter that cannot be resolved on the basis of evidence from Langebaanweg. There is, however, little doubt that a generally acceptable date, probably 5,2 Ma (see Van Couvering 1978), will result from the many investigations relevant to this question. The same applies in the case of the duration of the early Pliocene transgression. Judging from evolutionary changes manifested in certain mammalian taxa common to more than one level of the QSM and PPM (see p. 24), the phase of the transgression represented by these deposits might have been in the order of many millennia, while the transgression as a whole could conceivably have lasted several hundred thousand years.

Until these issues are resolved, it will be convenient to use the 5 Ma estimate suggested above in reference to the deposits in the Langebaanweg area that date from the early Pliocene transgression (i.e. the QSM, PPM and Anyskop marine deposits).

There are more marked differences of opinion over the dating of the Pliocene–Pleistocene boundary, and these have a bearing on the inferred chronometric dates of the later elements in the Langebaanweg succession, particularly the Baard's Quarry fluviatile deposits. In recent years it has become common practice to date the Pliocene–Pleistocene boundary at either 1,8 Ma (e.g. Berggren & Van Couvering 1974), or 1,6 Ma (Haq et al. 1977). A contrasting opinion is that of Vail & Hardenbol (1979), who fixed this boundary at 2,8 Ma, which coincides with the termination of their sea-level cycle, TP3.

It was with an age range of 2-3 Ma in mind that the age of the Baard's Quarry fluviatile deposits fauna was suggested to be late Pliocene/early Pleistocene. It now appears that at least a part of this fauna is younger than 2 Ma, a conclusion that is based on the presence of Equus. According to Lindsay et al. (1980: 135) 'there were at least three major dispersal events of large mammals during the Pliocene (at 1,9, 2,6 and 3,7 Myr)', with Equus having dispersed into Africa during the 1,9 Ma event. The Baard's Quarry fluviatile deposits, therefore, cannot be older than 1,9 Ma, and are more likely to date from sea-level cycle QI than cycle TP3 (see p. 41).

This raises another problem concerning the fauna of these deposits. There are other elements in the assemblage that would be more consistent with an age

of more than 2 Ma. This was discussed by Hendey (1978*a*) and Gentry (1980), and it now seems that the possible temporal heterogeneity of this fauna was dismissed too lightly in the former study. The composition of this fauna can be most readily explained by the hypothesis that while the deposits themselves date from cycle Q1, they include both contemporary fossils and others reworked from pre-existing Pliocene deposits.

There are thus several issues relating to the age of the post-Varswater Formation deposits in the Langebaanweg area that have yet to be settled, while the chronometric ages of all elements in the succession have also to be established. In addition, Vail & Hardenbol (1979: 79) concede that there 'is no question that considerably more research needs to be undertaken to document the magnitudes and timing of eustatic sea-level changes'. Nevertheless, little significance is attached to the present uncertainties concerning details of the Laangebaanweg succession and global sea-level changes. The agreement between them is sufficient to justify the conclusion that the former can for the most part be regarded as securely dated in a geological sense. At the very least, there is now a sound basis on which future research on dating can be based.

In conclusion, it should be mentioned that botanical evidence of age is potentially available for certain elements in the succession, although for the present and in the immediate future the faunal and geological dating of the Langebaanweg sequence will provide data for palaeobotanical sudies. A tentative 'Pollen Zone' sequence for the south-western Cape has already been established (Coetzee 1978), and there is apparently considerable potential for refining this scheme (J. A. Coetzee, pers. comm.). The existing pollen sequence is only tentatively correlated with the 'E' Quarry succession (Table 8).

SUMMARY AND CONCLUSIONS

Cenozoic deposits in the vicinity of Langebaanweg are comprised largely of a late Tertiary succession of clastic sediments. They include economically important phosphate deposits and some immensely rich fossil occurrences. The history of this succession has been reinterpreted on the basis of geological and palaentological evidence, and it has been correlated with the record of South African west coast sea-level changes, for which successive shorelines at 30 m, 90 m, 50 m and 20 m above present sea-level are recognized. This interpretation is in accord with the global sea-level changes recorded by Vail & Hardenbol (1979).

The succession is as follows:

1. Basal element ('pre-GM deposits')—early to middle Miocene transgression (part of global sea-level cycles TM1.3, TM1.4, TM2.1 and TM2.2); terrestrial and marine complex.
2. No local record—middle to late Miocene regression (cycle TM2.3).
3. Gravel Member (GM) of the Varswater Formation—late Miocene regression (30 m shoreline—cycle TM3.1); marine beach complex.
4. No local record—terminal Miocene regression (cycles TM3.2, TM3.3).

5. Quartzose Sand Member (QSM) of the Varswater Formation—early Pliocene transgression (cycle TP1); estuarine complex with floodplain (QSM I), salt marsh (QSM II) and tidal flat (QSM III) facies.
6. Pelletal Phosphorite Member (PPM) of the Varswater Formation—early Pliocene transgression (cycle TP1); fluviatile (beds 3aS and 3aN) and marine littoral (PPM undifferentiated) complex.
7. Anyskop marine deposits—early Pliocene transgression (cycle TP1); coastal barrier complex.
8. Marine platform south-east of Langebaanweg—early Pliocene transgression (90 m shoreline—cycle TP1).
9. Anyskop terrestrial deposits—late Pliocene regression (50 m shoreline—cycle TP2).
10. Baard's Quarry fluviatile deposits—late Pliocene regression, or, more probably, early Pleistocene transgression (20 m shoreline—cycle TP3 or cycle Q1).

The local succession is completed by Quaternary deposits, including a nearly ubiquitous covering of aeolian sands. The area also has fossil occurrences and hominid occupation sites dating from the middle Pleistocene, late Pleistocene, and Holocene.

The nature of this succession was determined by the physical geography of the region, while the preservation of an unusually large body of early Pliocene sediment was due to the development of a coastal barrier complex, part of which survived subsequent erosion, and which protected underlying deposits.

Palaeontological investigations have centred on the Varswater Formation as it is exposed in an open-cast phosphate mine, 'E' Quarry. Some plant fossils are represented in these and underlying deposits, while about 230 invertebrate and vertebrate taxa, ranging from protozoans to mammals, have been recorded, mainly from the QSM and PPM. The fossils were recovered from a variety of marine, freshwater and terrestrial depositional environments. The species and body part representation, and the condition of specimens, was dependent on the source of the material.

Most of the collected invertebrates have been described, but the lower vertebrates are still largely unstudied. The birds evidently represent the largest pre-Pleistocene assemblage known anywhere, and they are also largely unstudied. The mammals are the most intensively studied and best represented group, although only about half of the eighty species recognized have been described. They range from shrews and mice to elephants and whales, and those already studied include four new genera and sixteen new species.

Detailed analyses of assemblages from the various depositional environments have yet to be undertaken. However, preliminary observations have revealed evidence for both subaerial and subaqueous deposition of material (e.g. in QSM 1, and in PPM, 3aN respectively). Individual specimens show signs of damage by such processes as carnivore activity (e.g. toothmarks, etching by stomach acids) and fires.

Late Tertiary environments contrast sharply with that of the present, which is semi-arid (summer dry/winter wet), with no naturally occurring surface freshwater, and with a rather sparse sclerophyll (fynbos) vegetation without indigenous trees. During the Miocene, tropical forests, possibly associated with a monsoon climate, existed in the area, but by the early Pliocene the environment was deteriorating. Temperatures had moderated from tropical to temperate, while precipitation had probably declined. Rainfall was then strongly seasonal, with a summer-wet/winter-dry pattern being likely. Wooded areas were probably restricted to the immediate vicinity of the river which was responsible for feeding in most of the sediment comprising the QSM and PPM. Grazing species amongst the mammalian herbivores indicate the presence of grasslands, and there is palynological evidence for the presence of fynbos vegetation types. However, woodland browsers still formed a significant element in the mammalian fauna, although dental abnormalities indicate stresses in these populations which might have been due to the diminution of suitable habitats, and aggravated by factors such as droughts and fires.

The evidence for changing environments at Langebaanweg during the late Tertiary is in keeping with the record elsewhere in the word. This contributed to the correlation of the local succession with others elsewhere in the world (e.g. the Mediterranean Basin), which were also under the influence of such phenomena as changes in the volume of the Antarctic ice-cap.

The mammalian fauna of the QSM and PPM is in several respects 'intermediate' in character, which is in keeping with the environmental changes of the period in question. Although it is essentially 'African' in character, it includes descendants of several Miocene immigrants from Eurasia (e.g. the three-toed horse, *Hipparion*, and the bear, *Agriotherium*). The composition of certain groups (e.g. the hyaenas) still reflected a pattern more characteristic of the Miocene than the Quaternary. However, early representatives of successful Quaternary lineages are recorded (e.g. the white rhinoceros, *Ceratotherium*). While individual taxa represent advances over their Miocene ancestors, many were much less specialized than their Quaternary descendants (e.g. the seal, *Homiphoca capensis*). Some 'tropical' elements were still present (e.g. parrots, giraffes), but the moderating climate might already have caused some to become extinct, or nearly extinct (e.g. crocodiles, primates).

Faunal evidence of age is in good accord with the geological evidence, although absolute, or chronometric, dates for the various elements in the succession are still lacking.

In a little more than a decade the Langebaanweg succession has become one of the more intensively studied and best understood complexes of late Tertiary deposits in southern Africa. It has also become the source of the largest assemblage of late Tertiary vertebrates known anywhere in Africa. The unique set of geological, botanical and faunal data already available have combined to provide an unparalleled insight into the nature of local late Tertiary environments and the changes that they underwent. In spite of all this,

there is still a considerable potential for further research, and the significance of this area in southern African Cenozoic studies should increase still further.

ACKNOWLEDGEMENTS

REFERENCES

ANONYMOUS, 1975. Données sur quelques localités à mammifères d'Âge Néogène supérieur du Languedoc. *Act. I Col. Intern. Sobre Biostrat. Cont. Neogeno Sup. Cuat. Inf.* **4**: 23–29.
AXELROD, D. I. & RAVEN, P. V. 1978. Late Cretaceous and Tertiary vegetation history of Africa. *In*: WERGER, M. J. A. ed. *Biogeography and ecology of southern Africa*: 77–130. The Hague: W. Junk.
AZZAROLI, A. 1975. Late Miocene interchange of terrestrial faunas across the Mediterranean. *Act. I Col. Intern. Sobre Biostrat. Cont. Neogeno Sup. Cuat. Inf.* **4**: 67–71.
BASS, A. J., D'AUBREY, J. D. & KISTNASAMY, N. 1973. Sharks of the east coast of southern Africa. I. The genus *Carcharhinus* (Carcharhinidae). *Invstl Rep. oceanogr. Res. Inst. Durban* **33**: 1–168.
BASS, A. J., D'AUBREY, J. D. & KISTNASAMY, N. 1975. Sharks of the east coast of southern Africa. V. The families Hexanchidae, Chlamydoselachidae, Heterodontidae, Pristiophoridae and Squatinidae. *Invstl Rep. oceanogr. Res. Inst. Durban* **43**: 1–50.
BEHRENSMEYER, A. K. 1976. Lothagam, Kanapoi and Ekora: A general summary of stratigraphy and fauna. *In*: COPPENS, Y. *et al.* eds. *Earliest man and environments in the Lake Rudolf Basin*: 163–170. Chicago: University Press.
BERGGREN, W.A. & VAN COUVERING, J. A. 1974. *The Late Neogene*. Amsterdam: Elsevier.

BIRCH, G. F. 1977. Phosphorites from the Saldanha Bay region. *Trans. R. Soc. S. Afr.* **42**: 223–240.

BISHOP, W. W. 1980. Palaeogeography and continental taphonomy. *In:* BEHRENSMEYER, A. K. & HILL, A. P. eds. *Fossils in the making*: 20–37. Chicago: University Press.

BOAZ, N. T., GAZIRY, A. W. & EL-ARNAUTI, A. 1979. New fossil finds from the Libyan Upper Neogene site of Sahabi. *Nature, Lond.* **280**: 137–139.

BONÉ, E. L. & SINGER, R. 1965. *Hipparion* from Langebaanweg, Cape Province and a revision of the genus in Africa. *Ann. S. Afr, Mus.* **48**: 273–397.

BOUCHER, C. & JARMAN, M. L. 1977. The vegetation of the Langebaan area, South Africa. *Trans. R. Soc. S. Afr.* **42**: 241–272.

BROWN, A. C. & JARMAN, N. 1978. Coastal marine habitats. *In:* WERGER, M. J. A. ed. *Biogeography and ecology of southern Africa*: 1239–1277. The Hague: W. Junk.

BUTZER, K. W. 1973. On the sedimentary sequence from the 'E' Quarry, Langebaanweg, Cape Province. *Quaternaria* **17**: 237–243.

CARRINGTON, A. J. & KENSLEY, B. F. 1969. Pleistocene molluscs from the Namaqualand coast. *Ann. S. Afr. Mus.* **52**: 189–223.

CARTER, A. N. 1978. Phosphatic nodule beds in Victoria and the late Miocene–Pliocene eustatic event. *Nature, Lond.* **276**: 258–259.

CHURCHER, C. S. 1978. Giraffidae. *In:* MAGLIO, V. J. & COOKE, H. B. S. eds. *Evolution of African mammals*: 509–535. Cambridge, Mass.: Harvard University Press.

CHURCHER, C. S. & RICHARDSON, M. L. 1978. Equidae. *In:* MAGLIO, V. J. & COOKE, H. B. S. eds. *Evolution of African mammals*: 379–422. Cambridge, Mass.: Harvard University Press.

COETZEE, J. A. 1978. Late Cainozoic palaeoenvironments of southern Africa. *In:* VAN ZINDEREN BAKKER, E. M. ed. *Antarctic glacial history and world palaeoenvironments*: 115–127. Rotterdam: Balkema.

COOKE, H. B. S. & WILKINSON, A. F. 1978. Suidae and Tayassuidae. *In:* MAGLIO, V. J. & COOKE, H. B. S. eds. *Evolution of African mammals*: 435–482. Cambridge, Mass.: Harvard University Press.

COPPENS, Y., MAGLIO, V. J., MADDEN, C. T. & BEDEN, M. 1978. Proboscidea. *In:* MAGLIO, V. J. & COOKE, H. B. S. eds. *Evolution of African mammals*: 336–367. Cambridge, Mass.: Harvard University Press.

CORVINUS, G. & HENDEY, Q. B. 1978. A new Miocene vertebrate locality at Arrisdrift in Namibia (South West Africa). *N. Jb. Geol. Palaont. Mh.* **1978**: 193–205.

CORYNDON, S. C. 1978. Hippopotamidae. *In:* MAGLIO, V. J. & COOKE, H. B. S. eds. *Evolution of African mammals*: 483–495. Cambridge, Mass.: Harvard University Press.

DAVIES, O. 1972. Pleistocene shorelines in the southern and south-eastern Cape Province (2). *Ann. Natal Mus.* **21**: 225–279.

DAVIES, O. 1973. Pleistocene shorelines in the western Cape and South West Africa. *Ann. Natal Mus.* **21**: 719–765.

DAY, J. H. 1974. *A guide to marine life on South African shores*. Cape Town: Balkema.

DEACON, H. J. 1979. Palaeocology. *In:* DAY, J., SIEGFRIED, W. R., LOUW, G. N. & JARMAN, M. L. eds. *Fynbos ecology: a preliminary synthesis*: 58–69. Pretoria: *S. Afr. natn. scient. Progm. Rep.* **40**.

DELSON, E. 1975. Paleoecology and zoogeography of the Old World monkeys. *In:* TUTTLE, R. H. ed. *Primate functional morphology and evolution*: 37–64. The Hague: Mouton.

DINGLE, R. V. 1971. Tertiary sedimentary history of the continental shelf off southern Cape Province, South Africa. *Trans. geol. Soc. S. Afr.* **74**: 173–186.

DINGLE, R. V. 1973. The geology of the continental shelf between Lüderitz and Cape Town (south-west Africa), with special reference to Tertiary strata. *J. geol. Soc. Lond.* **129**: 337–363.

DINGLE, R. V., LORD, A. R. & HENDEY, Q. B. 1979. New sections in the Varswater Formation (Neogene) of Langebaan Road, south-western Cape, South Africa. *Ann. S. Afr. Mus.* **78**: 81–92.

DORST, J. & DANDELOT, P. 1970. *A field guide to the larger mammals of Africa*. London: Collins.

FUGGLE, R. F. & ASHTON, E. R. 1979. Climate. *In:* DAY, J., SIEGFRIED, W. R., LOUW, G. N. & JARMAN, M. L. eds. *Fynbos ecology: a preliminary synthesis*: 7–15. Pretoria: *S. Afr. natn. scient. Progm. Rep.* **40**.

GENTRY, A. W. 1974. A new genus and species of Pliocene boselaphine (Bovidae, Mammalia) from South Africa. *Ann. S. Afr. Mus.* **65**: 145–188.

GENTRY, A. W. 1978. Bovidae. *In:* MAGLIO, V. J. & COOKE, H. B. S. *eds. Evolution of African mammals:* 540–572. Cambridge, Mass.: Harvard University Press.

GENTRY, A. W. 1980. Fossil Bovidae (Mammalia) of Langebaanweg, South Africa. *Ann. S. Afr. Mus.* **79**: 213–337.

GILL, E.D. 1975. Evolution of Australia's unique flora and fauna in relation to the plate tectonics theory. *Proc. R. Soc. Victoria* **87**: 215–234.

GOLPE-POSSE, J.-M. 1977. *Barberahyus castellensis* n. g. n. sp., Tayasuido del Vindoboniense terminal de Castell de Barberà (Cuenca del Vallès, Espana). *Paleont. Evoluc.* **12**: 31–43.

GREENWAY, P. J. 1970. A classification of the vegetation of east Africa. *Kirkia* **9**: 1–68.

HALLAM, C. D. 1964. The geology of the coastal diamond deposits of southern Africa (1959). *In:* HAUGHTON, S. H. *ed. The geology of some ore deposits in southern Africa* **2**: 671–728. Johannesburg: Geological Society of South Africa.

HAMILTON, W. R. & VAN COUVERING, J. A. 1977. Lower Miocene mammals of South West Africa. *Namib Bull. (Suppl. 2, Transv. Mus. Bull.):* 9–11.

HAQ, B. U., BERGGREN, W. A. & VAN COUVERING J. A. 1977. Corrected age of the Pliocene/Pleistocene boundary. *Nature, Lond.* **269**: 483–488.

HARRIS, J. M. 1976. Pliocene Giraffoidea (Mammalia, Ariodactyla) from the Cape Province. *Ann. S. Afr. Mus.* **69**: 325–353.

HARRIS, J. M. & WHITE, T. D. 1979. Evolution of the Plio-Pleistocene African Suidae. *Trans. Am. phil. Soc* **69** (2): 1–128.

HARRISON, A. D. 1964. An ecological survey of the Great Berg River. *In:* DAVIS, D. H. S. *ed. Ecological studies in southern Africa:* 143–158. The Hague: W. Junk.

HARRISON, A. D. & ELSWORTH, J. F. 1958. Hydrobiological studies on the Great Berg River, Western Cape Province. Part 1. A general description, chemical studies on the water and main features of the fauna and flora. *Trans R. Soc. S. Afr.* **35**: 125–226.

HAUGHTON, S. H. 1968. *Geological history of southern Africa.* Johannesburg: Geological Society of South Africa.

HAYES, M. O. 1976 Beaches–barrier islands. *In:* HAYES, M. O. & KANA, T. W. *eds. Terrigenous clastic depositional environments:* I 81–I 108. Columbia, SC: University of South Carolina.

HAYES, D. E., FRAKES, L. A., BARRETT, P., BURNS, D. A., CHEN, P. H., FORD, A. S., KANEPS, A. G., KEMP, E. A., McCOLLUM, D. W., PIPER, D. J. W., WALL, W. E. & WEBB, P. N. 1973. Leg 28 deep-sea drilling in the Southern Ocean. *Geotimes* **18** (6): 19–24.

HENDEY, Q. B. 1969. Quaternary vertebrate fossil sites in the south-western Cape Province. *S. Afr. archaeol. Bull.* **24**: 96–105.

HENDEY, Q. B. 1970a. A review of the geology and palaeontology of the Plio/Pleistocene deposits at Langebaanweg, Cape Province. *Ann. S. Afr. Mus.* **56**: 75–117.

HENDEY, Q. B. 1970b. The age of the fossiliferous deposits at Langebaanweg, Cape Province. *Ann. S. Afr. Mus.* **56**: 119–131.

HENDEY, Q. B. 1972a. A Pliocene ursid from South Africa. *Ann. S. Afr. Mus.* **59**: 115–132.

HENDEY, Q. B. 1972b. Further observations on the age of the mammalian fauna from Langebaanweg, Cape Province. *Palaeoecol. afr.* **6**: 172–175.

HENDEY, Q. B. 1973. Fossil occurrences at Langebaanweg, Cape Province. *Nature, Lond.* **244**: 13–14.

HENDEY, Q. B. 1974a. The late Cenozoic Carnivora of the south-western Cape Province. *Ann. S. Afr. Mus.* **63**: 1–369.

HENDEY, Q. B. 1974b. Faunal dating of the late Cenozoic of southern Africa, with special reference to the Carnivora. *Quaternary Res.* **4**: 149–161.

HENDEY, Q. B. 1976a. The Pliocene fossil occurrences in 'E' Quarry, Langebaanweg, South Africa. *Ann. S. Afr. Mus.* **69**: 215–247.

HENDEY, Q. B. 1976b. Fossil peccary from the Pliocene of South Africa. *Science* **192**: 787–789.

HENDEY, Q. B. 1977. Fossil bear from South Africa. *S. Afr. J. Sci.* **73**: 112–116.

HENDEY, Q. B. 1978a. The age of the fossils from Baard's Quarry, Langebaanweg, South Africa. *Ann. S. Afr. Mus.* **75**: 1–24.

HENDEY, Q. B. 1978b. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Ann. S. Afr. Mus.* **76**: 1–41.

HENDEY, Q. B. 1978c. Late Tertiary Hyaenidae from Langebaanweg, South Africa, and their relevance to the phylogeny of the family. *Ann. S. Afr. Mus.* **76**: 265–297.

HENDEY, Q. B. 1978d. Late Tertiary Mustelidae (Mammalia, Carnivora) from Langebaanweg, South Africa. *Ann. S. Afr. Mus.* **76**: 329–357.

HENDEY, Q. B. 1980. *Agriotherium* (Mammalia, Ursidae) from Langebaanweg, South Africa, and relationships of the genus. *Ann. S. Afr. Mus.* **81**: 1–109.

HENDEY, Q. B. & REPENNING, C. A. 1972. A Pliocene phocid from South Africa. *Ann. S. Afr. Mus.* **59**: 71–98.

HOOIJER, D. A. 1972. A late Pliocene rhinoceros from Langebaanweg, Cape Province. *Ann. S. Afr. Mus.* **59**: 151–191.

HOOIJER, D. A. 1976. The late Pliocene Equidae of Langebaanweg, Cape Province, South Africa. *Zool. Verh.* **148**: 1–39.

HOOIJER, D. A. 1978. Rhinocerotidae. *In:* MAGLIO, V. J. & COOKE, H. B. S. *eds. Evolution of African mammals*: 371–378. Cambridge, Mass.: Harvard University Press.

HOOIJER, D. A. & MAGLIO, V. J. 1974. Hipparions from the late Miocene and Pliocene of northwestern Kenya. *Zool. Verh.* **134**: 1–34.

HOPWOOD, A. T. 1928. New and little known mammals from the Miocene of Africa. *Am. Mus. Novit.* **344**: 1–9.

HSÜ, K. J., MONTADERT, L., BERNOULLI, D., CITA, M. B., ERICKSON, A., GARRISON, R. E., KIDD, R. B., MÈLIERÉS, F., MÜLLER, C. & WRIGHT, R. 1977. History of the Mediterranean salinity crises. *Nature, Lond.* **267**: 399–403.

KEMP, E. M. 1978. Tertiary climatic evolution and vegetation history in the southeast Indian Ocean region. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* **24**: 169–208.

KENNETT, J. P. 1978. Cainozoic evolution of circumantarctic palaeoceanography. *In:* VAN ZINDEREN BAKKER, E. M. *ed. Antarctic glacial history and world palaeoenvironments*: 41–56. Rotterdam: Balkema.

KENSLEY, B. 1972. Pliocene marine invertebrates from Langebaanweg, Cape Province. *Ann. S. Afr. Mus.* **60**: 173–190.

KENSLEY, B. 1973. *Sea-shells of southern Africa. Gastropods.* Cape Town: Maskew Miller.

KENSLEY, B. 1977. A second assemblage of Pliocene invertebrate fossils from Langebaanweg, Cape. *Ann. S. Afr. Mus.* **72**: 189–210.

KING, J. E. 1964. *Seals of the world*. London: British Museum (Natural History).

KLEIN, R. G. 1975. Paleoanthropological implications of the non-archaeological bone assemblage from Swartklip 1, south-western Cape Province, South Africa. *Quaternary Res.* **5**: 275–288.

KLEIN, R. G. 1980. Environmental and ecological implications of large mammals from Upper Pleistocene and Holocene sites in southern Africa. *Ann. S. Afr. Mus.* **81**: 223–283.

KÖPPEN, W. & GEIGER, R. 1936. *Handbuch der Klimatologie*. Berlin: Borntraeger.

KRÖNINGER, H. 1978. National Lightning Recording Scheme. *Newsl. natn. Elect. Engng Res. Inst. (CSIR):* 1–18.

KRUGER, F. J. 1979. Fire. *In:* DAY, J., SIEGFRIED, W. R., LOUW, G. N. & JARMAN, M. L. *eds. Fynbos ecology: a preliminary synthesis*: 43–57. Pretoria. *S. Afr. natn. scient. Progm. Rep.* **40**.

KRUMBEIN, W. C. & SLOSS, L. L. 1963. *Stratigraphy and sedimentation*. San Francisco: W. H. Freeman.

KURTÉN, B. 1971. *The Age of Mammals*. London: Weidenfeld & Nicolson.

LAMONT, G. 1947. The geology of part of the Vanrhynsdorp Division, Cape Province. University of Cape Town: Unpublished Ph. D. thesis.

LEVYNS, M. R. 1964. Migrations and origins of the Cape Flora. *Trans. R. Soc. S. Afr.* **37**: 85–107.

LINDSAY, E. H., OPDYKE, N. D. & JOHNSON, N. M. 1980. Pliocene dispersal of the horse *Equus* and late Cenozoic mammalian dispersal events. *Nature, Lond.* **287**: 135–138.

LOBREAU-CALLEN, D. & SUC, J.-P. 1972. Présence de pollens de *Microtropus fallax* (Celastraceae) dans le Pleistocène inférieur de Celleneuve (Hérault). *C.r. hebd. Séanc. Acad. Sci. Paris* (D) **275**: 1351–1354.

LOUTIT, T. S. & KENNETT, J. P. 1979. Application of carbon isotope stratigraphy to Late Miocene shallow marine sediments, New Zealand. *Science* **204**: 1196–1199.

MABBUTT, J. A. 1956. The physiography and surface geology of the Hopefield fossil site. *Trans. R. Soc. S. Afr.* **35**: 21–58.

MAGLIO, V. J. 1973. Origin and evolution of the Elephantidae. *Trans. Am. phil. Soc.* **63**: 1–149.

MAGLIO, V. J. 1978. Patterns of faunal evolution. *In:* MAGLIO, V. J. & COOKE, H. B. S. *eds. Evolution of African mammls* 603–619. Cambridge, Mass.: Harvard University Press.

MAGLIO, V. J. & HENDEY, Q. B. 1970. New evidence relating to the supposed stegolophodont ancestry of the Elephantidae. *S. Afr. archaeol. Bull.* **25**: 85–87.

McKENNA, M. C. 1973. Sweepstakes, Filters, Corridors, Noah's Arks, and Beached Viking Funeral Ships in palaeogeography. *In:* TARLING, D. H. & RUNCORN, S. K. eds. *Implications of Continental Drift to the Earth Sciences* **1**: 295–308. London: Academic Press.

McLACHLAN G.R. & LIVERSIDGE, R. 1978. *Roberts birds of South Africa.* Cape Town: The John Voelcker Bird Book Fund.

McLACHLAN, I. R. & McMILLAN, I. K. 1979. Microfaunal biostratigraphy, chronostratigraphy, and history of Mesozoic and Cenozoic deposits on the coastal margin of South Africa. *Spec. Publs. Geol. Soc. S. Afr.* **6**: 161–182.

MERCER, J. H. 1978. Glacial development and temperature trends in the Antarctic and in South America. *In:* VAN ZINDEREN BAKKER, E. M. ed. *Antarctic glacial history and world palaeoenvironments*: 73–93. Rotterdam: Balkema.

MUIZON, C. DE & HENDEY, Q. B. 1980. Late Tertiary seals of the South Atlantic Ocean. *Ann. S. Afr. Mus.* **82**: 91–128.

OLSON, E. C. 1962. Late Permian terrestrial vertebrates, USA and USSR. *Trans. Am. phil. Soc.* **52** (2): 3–224.

PATTERSON, B., BEHRENSMEYER, A. K. & SILL, W. D. 1970. Geology and fauna of a new Pliocene locality in north-western Kenya. *Nature, Lond.* **226**: 918–921.

POCOCK, T. N. 1976. Pliocene mammalian microfauna from Langebaanweg: A new fossil genus linking the Otomyinae with the Murinae. *S. Afr. J. Sci.* **72**: 58–60.

RICH, P. V. 1980. Preliminary report on the fossil avian remains from Late Tertiary sediments at Langebaanweg (Cape Province), South Africa. *S. Afr. J. Sci.* **76**: 166–170.

ROGERS, J. 1980. First report on the Cenozoic sediments between Cape Town and Elands Bay. *Rep. geol. Surv. S. Afr.* **1980–165**: 1–64. (Open file.)

SCHULZE, B. R. 1965. *Climate of South Africa.* **8**. *General Survey.* Pretoria: Government Printer.

SCHULZE, R. E. & McGEE, O. S. 1978. Climatic indices and classifications in relation to biogeography of southern Africa. *In:* WERGER, M. J. A. ed. *Biogeography and ecology of southern Africa*: 19–52. The Hague: W. Junk.

SCOTT, J. H. & SYMONS, N. B. B. 1974. *Introduction to dental anatomy.* Edinburgh & London: Churchill Livingstone.

SHACKLETON, N. J. & OPDYKE, N. D. 1973. Oxygen isotope and palaeomagnetic stratigraphy of Equatorial Pacific Core V28–238; Oxygen isotope temperatures and ice volumes on a 10^5 and 10^6 year scale. *Quaternary Res.* **3**: 39–55.

SIESSER, W. G. 1978. Age of phosphorites on the South African continental margin. *Marine Geol.* **26**: M17–M28.

SIESSER, W. G. & DINGLE, R. V. 1981. Tertiary sea-level movements around southern Africa. *J. Geol* **89**: 83–96.

SIMPSON, G. G. 1967. *The geography of evolution.* New York: Capricorn Books.

SIMPSON, G. G. 1971. Fossil penguin from the late Cenozoic of South Africa. *Science* **171**: 1144–1145.

SIMPSON, G. G. 1975. Notes on variation in penguins and on fossil penguins from the Pliocene of Langebaanweg, Cape Province, South Africa. *Ann. S. Afr. Mus.* **69**: 59–72.

SIMPSON, G. G. 1976. *Penguins. Past and present, here and there.* New Haven: Yale University Press.

SIMPSON, G. G. 1979. A new genus of late Tertiary penguin from Langebaanweg, South Africa. *Ann. S. Afr. Mus.* **78**: 1–9.

SINGER, R. 1961. The new fossil sites at Langebaanweg (South Africa). *Curr. Anthrop* **2**: 385–387.

SINGER, R. & HOOIJER, D.A. 1958. A *Stegolophodon* from South Africa. *Nature, Lond.* **182**: 101–102.

STROMER, E. 1926. Reste land- und süsswasser bewohnender Wirbeltiere aus den Diamantenfeldern Deutsch-Südwestafrikas. *In:* KAISER, E. ed. *Die Diamantenwüste Südwestafrikas* **2**: 107–153. Berlin: D. Reimer.

STROMER, E. 1931a. Reste süsswasser- und land bewohnender Wirbeltiere aus den Diamantenfelden Klein-Namaqualandes (Südwest-afrika). *Sber. bayer Akad. Wiss.* **1931**: 17–47.

STROMER, E. 1931b. *Palaeothentoides africanus*, nov. gen., nov. spec., ein erstes Beuteltier aus Afrika. *Sber. bayer. Akad. Wiss.* **1931**: 177–190.

TANKARD, A. J. 1974a. Varswater Formation of the Langebaanweg–Saldanha area, Cape Province. *Trans. geol. Soc. S. Afr.* **77**: 265–283.

TANKARD, A. J. 1974b. Petrology and origin of the phosphate and aluminium phosphate rock of the Langebaanweg–Saldanha area, south-western Cape Province. *Ann. S. Afr. Mus.* **65**: 217–249.

TANKARD, A. J. 1975a. The marine Neogene Saldanha Formation. *Trans. geol. Soc. S. Afr.* **78**: 257–264.

TANKARD, A. J. 1975b. The late Cenozoic history and palaeoenvironments of the coastal margin of the south-western Cape Province, South Africa. Rhodes University: Unpublished Ph. D. thesis.

TANKARD, A. J. 1975c. Varswater Formation of the Langebaanweg–Saldanha area, Cape Province. (Discussion.) *Trans. geol. Soc. S. Afr.* **78**: 373–375.

TANKARD, A. J. 1975d. Thermally anomalous Late Pleistocene molluscs from the south-western Cape Province, South Africa. *Ann. S. Afr. Mus.* **69**: 17–45.

TANKARD, A. J. 1976. Pleistocene history and coastal morphology of the Ysterfontein–Elands Bay area, Cape Province. *Ann. S. Afr. Mus.* **69**:73–119.

TANKARD, A. J. & ROGERS, J. 1978. Late Cenozoic palaeoenvironments on the west coast of southern Africa. *J. Biogeogr.* **5**: 319–337.

TAYLOR, H. C. 1978. Capensis. *In:* WERGER, M. J. A. ed. *Biogeography and ecology of southern Africa*: 171–229. The Hague: W. Junk.

THOMAS, H. 1979. *Miotragocerus cyrenaicus* sp. nov. (Bovidae, Artiodactyla, Mammalia) du Miocène supérieur de Sahabi (Libye) et ses rapports avec les autres *Miotragocerus*. *Geobios* **12**: 267–281.

VAIL, P. R. & HARDENBOL, J. 1979. Sea-level changes during the Tertiary. *Oceanus* **22**: 71–79.

VAIL, P. R. MITCHUM, R. M. & THOMPSON, S. 1977. Seismic stratigraphy and global changes in sea level. Part 4: Global cycles of relative changes of sea level. *Mem. Am. Ass. Petrol. Geol.* **26**: 83-97.

VAN COUVERING, J. A. 1972. Radiometric calibration of the European Neogene. *In:* BISHOP, W. W. & MILLER, J. A. eds. *Calibration of hominoid evolution*: 247–271. Edinburgh: Scottish Academic Press.

VAN COUVERING J. A. 1978. Status of late Cenozoic boundaries. *Geology* **6**: 169.

VAN COUVERING, J. A. & BERGGREN, W. A. 1977. Biostratigraphical basis of the Neogene time scale. *In:* KAUFFMANN, E. G. & HAZEL, J. E. eds. *Methods of biostratigraphy*: 283–306. Stroudsburg, Pa.: Dowden, Hutchinson & Ross.

VAN COUVERING, J. A. BERGGREN, W. A., DRAKE, R. E., AGUIRRE, E. & CURTIS, G. H. 1976. The terminal Miocene event. *Mar. Micropaleontol.* **1**: 163–286.

VISSER, H. N. & SCHOCH, A. E. 1973. The geology and mineral resources of the Saldanha Bay area. *Mem. geol. Surv. S. Afr.* **63**: 1–150.

VOORHIES, M. R. 1969. Taphonomy and population dynamics of an Early Pliocene vertebrate fauna, Knox County, Nebraska. *Univ. Wyoming, Contr. Geol., Spec. Paper* **1**: 1–69.

WEBB, S. D. 1977. A history of savannah vertebrates in the New World. 1. North America. *A. Rev. Ecol. Syst.* **8**: 355–380.

WHITE, T. D. & HARRIS, J. M. 1977. Suid evolution and correlation of African hominid localities. *Science* **198**: 13–21.

WOLFF, R. G., SINGER, R. & BISHOP, W. W. 1973. Fossil bear (*Agriotherium* Wagner, 1837) from Langebaanweg, Cape Province, South Africa. *Quaternaria* **17**: 209–236.